JOURNAL

OF

HELMINTHOLOGY

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VOLUME X., 1932.

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CONTENTS OF VOLUME X.

No. 1 (FEBRUARY, 1932).

IMPERIAL BUREAU OF AGRICULTURAL PARASITOLOGY.

NOTES AND MEMORANDA.

Nos. 2-3 (JUNE, 1932).

Contents.

No. 4 (SEPTEMBER, 1932).

Journal of Helminthology, Vol. x, *No.* 1, *February*, 1932, *pp.* 1-14.

Helminths from Cyprus.

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This collection of parasites was made in Cyprus between February 1928 and August 1929. Some were collected by Professor R. T. Leiper personally while on a visit, the remainder were sent to the Helminthology Department of the London School of Hygiene and Tropical Medicine by Dr. R. J. Roe of the Civil Veterinary Department in Cyprus. The two collections are here dealt with together. The hosts from which the parasites were taken are as follows :—horse, mule, pig, dog, cat, sheep, goat, hedgehog and fowl. Altogether the collection comprises 16 genera and 21 species of Nematoda : 5 genera and 7 species of Cestoda : and some acanthocephala, linguatulids, ticks and sarcocysts. The latter three are not dealt with here. The following is a systematic survey of the specimens.

NEMATODES.

The Nematodes included in the collection comprise the following :—

Fam. : *Trichuridæ* Railliet, 1915.
Sub-fam. : *Trichurinæ* Ransom, 1911.

Genus : Trichuris Roederer, 1761.

The whipworms are here represented by 4 specimens of *T. ovis* (Abildg., 1795) from the cæcum of a goat. This is the common whipworm of domestic and wild ruminants. The material comprises one male, two females and one damaged specimen.

Fam: *STRONGYLIDÆ* Baird, 1853.
Sub-fam: *STRONGYLINÆ* Railliet, 1893.

Genus: STRONGYLUS Müller, 1780.

There are two species of this genus included. *S. edentatus* (Looss, 1900) is represented by a large number of worms of both sexes from the large and small intestines, stomach and cæcum of horses. The buccal capsule is without teeth. *S. vulgaris* (Looss, 1900), by ten specimens from the cæcum and large intestine of the horse. Two dorsal teeth are present. Both species are recorded from Egypt by Looss (1901, pp. 77-78).

Sub-fam.: *ŒSOPHAGOSTOMINÆ* Railliet, 1915.

Genus: ŒSOPHAGOSTOMUM Molin, 1861.

Two species are included in the collection. *Œ. dentatum* (Rudolphi, 1803), well preserved specimens of both sexes from the large intestine of the pig. *Œ. venulosum* (Rud. 1809). Males and females from the large intestine of a goat. Both these species are of common and cosmopolitan occurrence.

Fam.: *TRICHOSTRONGYLIDÆ* Leiper, 1912.
Sub-fam: *TRICHOSTRONGYLINÆ* Leiper, 1908.

Genus: TRICHOSTRONGYLUS Looss, 1905.

One species only; this is *T. vitrinus* Looss, 1905. The specimens are contained in the duodenal contents of a goat. *T. vitrinus* belongs among those species of *Trichostrongylus* in which the spicules are equal in size. Other recorded hosts include sheep and camel and also man. It is known to occur in Egypt (Looss, 1905, p. 421).

Genus: OSTERTAGIA Ransom, 1907.

O. circumcincta (Stadelmann, 1894). The specimens are from the small intestine of a sheep in which it is a very common parasite. Three other females of *Ostertagia* from the stomach of a goat can probably be also assigned to this species.

Fam.: *PROTOSTRONGYLIDÆ* Leiper, 1926.
Sub-fam.: *PROTOSTRONGYLINÆ* Kamensky, 1905.

Genus: METASTRONGYLUS Molin, 1861.

Females only present. These were taken from the bronchi of a pig, and are in all probability *M. apri* (Gmelin, 1790) [= *M. elongatus* (Duj., 1845).] Its distribution is cosmopolitan.

Genus: PROTOSTRONGYLUS Kamensky, 1905.

By the law of priority those species hitherto included in the genus *Synthetocaulus* (Railliet and Henry, 1907) should be assigned to this genus (Leiper, p. 207). The specimens present include *P. ocreatus* (Railliet and Henry, 1907) represented by adult worms from the bronchi of a goat: and larvæ of some species of *Protostrongylus* in scrapings from a similar situation, also in a goat. Among these larvæ a single egg was seen.

Genus: ÆLEUROSTRONGYLUS Cameron, 1927.

Æ. abstrusus (Railliet, 1898). Cameron (1927 p. 55) erected this genus to contain *Synthetocaulus abstrusus* of the cat and also certain larval stages from the cat and the mouse, wrongly diagnosed by Leuckart as belonging to *Ollulanus tricuspis*. The present material contains numerous fragments of the lungs of cats infested with larvæ and developing embryos which were kindly identified by Dr. Cameron himself as belonging to this species. The tail of the larva has a characteristic shape figured in Cameron's paper (p. 57). Centres of infestation are delineated by irregular, soft, creamy-white necrotic patches in the pulmonary tissue. The pathogenic effect of this infection upon the lungs must have been severe.

Genus: DICTYOCAULUS Railliet and Henry, 1907.

D. filaria (Rud., 1809) is here represented by a large number of males and females in rather damaged condition from the bronchi of a ewe. This lungworm is a very common parasite of sheep in Palestine, as shown by its abundance in a collection of parasites from that country recently examined here. It is a frequent cause of verminous bronchitis in sheep.

The classification of the lungworms adopted here is that given by Leiper (p. 203).

Fam.: *ANCYLOSTOMIDÆ* (Looss, 1905) Lane, 1917.
Sub-fam.: *NECATORINÆ* Lane, 1917.

Genus: UNCINARIA Froelich, 1789.

This genus is here represented by four females of *U. stenocephala* (Railliet, 1884) one of the common hookworms of the dog. The exact position of the parasites in the host is not given, but they were found in a bottle of *Dipylidium*. It is a well-known form in Europe and North America.

Fam.: *ASCARIDÆ* Baird, 1853.

Sub-fam: *ASCARINÆ* (Railliet and Henry, 1912) Travassos, 1913.

Genus: TOXASCARIS Leiper, 1907.

This genus is represented by two specimens of *T. leonina* (Linstow, 1902) which were present in a large assortment of *Mesocestoides* from a dog.

Fam.: *SPIRURIDÆ* Oerley, 1885.
Sub-fam.: *SPIRURINÆ* Railliet, 1915.

Genus: SPIROCERCA Railliet and Henry, 1911.

S. sanguinolenta (Rud., 1819). The host is not given, but it is presumably a canine carnivore. The worms are present in the perivascular connective and adipose tissues. This is a common S. European species.

Genus: HABRONEMA Dies., 1861.

The specimens include a fairly large number of both sexes of *H. megastoma* (Rud., 1819) from a stomach wall cyst in a mare; and three females of *H. muscæ* (Carter, 1861), from the cæcum and small intestine of a horse. This species is transmitted by flies (Ransom, p. 11). A number of small nodules excised from the conjunctiva of a mule were sent, with a query, as *Habronema* nodules. After studying paraffin

sections of the nodules this diagnosis is provisionally confirmed on the basis of a single larval nematode found in one set of sections. Specific differentiation of the adult worms is based largely on the morphology of the buccal cavity (Ransom, p. 28).

Van Sacaghem (1915, p. 362) records similar granular dermatitis in horses in the lower Congo caused by the larvæ of *Filaria irritans*, and mentions the eyelid as one of the infected positions. Railliet and Henry (p. 695) show that van Sacaghem's *Filaria irritans* is a species of *Habronema*. In a second paper van Sacaghem (1917, p. 726) considers that the worm is *H. megastoma* or *H. microstoma* and that transmission is not direct but, as shown by Ransom (p. 11) for *H. muscæ*, by flies. He provides evidence for incriminating the common house fly and a *Stomoxys*, his chief point being, that the most heavily infected horses are those in clean stables infested with flies, rather than those browsing on manure strewn spots. Strong, Shattuck and Wheeler (p. 135) summarise the work of the above writers on this parasite, and record a single possible case in a horse examined by them in Amazonia. They, however, found only fragments of a nematode in the lesions examined. Quoting Le Cointe (p. 89) these three writers describe the lesions as being 3 cm. to 4 cm. in diameter, soft and spongy, and found in any part of the body, and containing fibrous and calcareous granules interspersed with furrows filled with a serous pus. The nodules in the present material are much smaller (1 mm. to 2 mm. in diameter) but are riddled with such channels containing a hyaline fluid.

The condition set up by these *Habronema* larvæ is known as " summer sore," "plaie d'été" or "esponja" on account of the seasonal appearance and texture of the lesions.

The microphotographs (see Plate) show the gallery through which the worm is progressing and the local infiltration in the immediate neighbourhood of the parasite with cells of the mononuclear series. The generalised œdematous reaction gives a reticulated appearance.

Sub-fam.: *GONGYLONEMINÆ* Hall, 1916.

Genus: GONGYLONEMA Molin, 1857.

G. pulchrum (Molin, 1857). Represented by a single female from the

cæcum of a horse. The more usual position is the œsophagus. Pigs and ruminants are more frequent hosts than equines. Baylis (p. 71) includes six previously distinct species under the name *G. pulchrum*.

Fam.: *HETERAKIDÆ* Railliet and Henry, 1914.
Sub-fam.: *SUBULURINÆ* Travassos, 1914.

Genus: SUBULURA Molin, 1860.

This collection contains two well preserved tubes of *S. brumpti* (Lopez Neyra, 1922) Cram, 1926, and a third lot rather badly preserved in whisky which, after very detailed comparison, are likewise assigned to this species, although they show certain resemblances to *S. differens*. Their deep yellow colour is doubtless due to the preservative. Only one male specimen was present in this lot. Cram (p. 113) gives the known distribution of *S. brumpti* as including Spain, N. America and Africa including Algeria. The writer has found *S. brumpti* in the collection from Palestine referred to above. It would therefore appear to be well distributed round the Mediterranean. All three lots are from fowls: in two cases from the cæcum, in the third case the location is not given.

Fam.: *OXYURIDÆ* Cobbold, 1864.
Sub-fam.: *OXYURINÆ* Hall, 1916.

Genus: OXYURIS Rud., 1803.

There are 15 specimens of this cosmopolitan parasite of equines in the collection. In one case the host is given as a horse, but the position is not stated. Nine of the 15 specimens were passed in the stool of a one-year-old foal. No males are present.

Fam.: *RICTULARIIDÆ* Railliet, 1916.
Sub-fam.: *RICTULARIINÆ* Hall, 1913.

Genus: RICTULARIA Froelich, 1802.

Three females of *R. cahirensis* (Jägerskiöld, 1904), from the intestine of a cat are included. This is the only feline species of *Rictularia*, and is known to occur in the Eastern Mediterranean lands.

CESTODES.

Fam.: *TÆNIIDÆ* Ludwig, 1886.

Genus: ECHINOCOCCUS Rud., 1801.

E. granulosus (Batsch, 1786). The echinococcus material comprises the following specimens:—Two pieces of intestinal wall from a dog with the adults *in situ* in the mucosa: young hydatid cyst in the liver of a sheep: free adults from a dog; and a very scanty infection of eggs in mucous scrapings. The frequent occurrence of hydatid in the lungs and liver of domestic ruminants in Palestine shows that the adult infection of dogs must be very common in this part of the world.

Genus: TÆNIA Linn, 1758.

This genus is here represented by three species: *T. hydatigena* (Pallas, 1766), by two specimens of *Cysticercus tenuicollis* from the peritoneum of a goat: and *T. tæniaeformis* (Batsch, 1786), of which a single adult specimen is included. The host is not given: it is typically a cat. Thirdly, there is a single very young specimen of *Cysticercus* sp. in the liver of a hedgehog. This specimen is too young for detailed diagnosis. It shows no rostellar hooks.

Fam.: *MESOCESTOIDIDÆ* Fuhrmann, 1907.

Genus: MESOCESTOIDES Vaillant, 1863.

M. lineatus (Goeze, 1782). The collection contains a great number of scoleces and strobilæ showing segments in all stages of development, from the dog and ? cat.

Genus: DITHYRIDIUM Rud., 1819.

This generic name is given to a group of larval cestodes which are considered to be immature Mesocestoididæ. The present material contains a large assortment of *D. elongatum* (Blumberg, 1882) from the pleural and abdominal cavities and mesentery of a cat. This is probably the "*Cysticercus elongatus*" described and figured by Blumberg (p. 147). Cadéac (p. 477) describes "dythridiosis" of the cat associated with the larvæ of *Mesocestoides lineatus*.

Fam.: *HYMENOLEPIDIDÆ* Railliet and Henry, 1909.

Sub-fam.: *DIPYLIDIINÆ* Stiles, 1896.

Genus: DIPYLIDIUM Leuckart, 1863.

D. caninum (Linn., 1758). Here represented by a large assortment from dogs and cats including migrating gravid segments from a puppy.

Genus: JOYEUXIA Lopez Neyra, 1927.

This genus was erected by Lopez Neyra in 1927 (p. 438) to include those species, hitherto described as *Dipylidium*, characterised by a large number of rostellar hooks, a small number of testicular lobes and only one egg in each capsule instead of the typical " egg nests " of *Dipylidium*. The genus is here represented by some specimens from the cat in which the measurements approximate closely to those given by Lopez Neyra for *J. chyzeri* (Diamare, 1892). These specimens are accordingly diagnosed as this species.

ACANTHOCEPHALA.

Order: ECHINORHYNCHIDEA Southwell and Macfie, 1924.

Fam.: *OLIGOCANTHORHYNCHIDÆ* Southwell and Macfie, 1924.

Genus: PROSTHENORCHIS Travassos, 1915.

This genus is represented by a single female worm which was lying loose in the intestinal lumen of a hedgehog. According to Travassos (p. 52) the only species of *Prosthenorchis* occurring in the European hedgehog is *P. erinacei* (Rud., 1783). The name of the hedgehog is not given, but it is assumed to be *Erinaceus europæus* L., and the worm is therefore diagnosed as *P. erinacei*. The above classification is that given by Thapar (p. 116).

Check List of Helminths recorded from Cyprus arranged under Hosts.

In 1929, Dr. R. J. Roe, by whom much of the material described here was collected, compiled the first list of parasites known to occur in Cyprus (p. 10). This list comprises 9 genera and species of Nematoda ; one genus of Trematoda and 6 genera, including 10 species, of Cestoda. A check list of parasitic worms hitherto recorded for Cyprus is appended, which brings the final number of recorded genera and species up to :—

Trematodes.—1 genus and species.

Nematodes.—20 genera and 25 species.

Cestodes.—9 genera and 12 species of which only 2, *Echinococcus granulosus* and *Tænia solium*, are so far recorded in both larval and adult stages : (or 3 if *Dithyridium elongatum* is really the larva of *Mesocestoides lineatus*).

Acanthocephala.—1 genus and species.

Hirudinacea.—1 genus and species (not identified).

Host.	*Parasite.*	*Position in Host.*
Man... ...	*T. solium*	—
	Tapeworm other than *T. solium* ...	—
	Echinococcus granulosus (hydatid cyst)	Liver, shoulder, spleen.
	" Roundworms "	—
	Leeches	Naso-pharynx.
Equines.		
Horse ...	*Ascaris megalocephala* (R) ...	—
	Habronema muscæ (S)	Cæcum and small intestine.
	Habronema megastoma (S) ...	Stomach wall cyst.
	Habronema sp. (R)	—
	Gongylonema pulchrum (S) ...	Cæcum.
	Oxyuris equi (S)	—

	Strongylus (*Delafondia*) *vulgaris* (S)	Cæcum and large intestine.
	Strongylus (*Alfortia*) *edentatus* (S)	Small intestine, stomach, cæcum.
Mule ...	*Trichonema catinatum* (R) ...	—
	? *Habronema* sp. (larva) (S) ...	Conjunctival nodule.
Donkey ...	*Habronema* sp. (R)	—

RUMINANTS.

Goat ...	*Œsophagostomum venulosum* (R and S)	Large intestine.
	Gongylonema verrucosum (R) ...	—
	Protostrongylus sp. (Larvæ) (S) ...	Bronchi.
	Protostrongylus ocreatus (S) ...	Bronchi.
	Ostertagia ? *circumcincta* (S) ...	Stomach.
	Trichostrongylus vitrinus (S) ...	Duodenum.
	Trichuris ovis (S)	Cæcum.
	Stilesia globipunctata or *Avitellina centripunctata* (R)	—
	Moniezia expansa sens lat. (R) (in Kid)	—
	Cysticercus tenuicollis (R and S) ...	Mesentery.
Sheep ...	*Ostertagia circumcincta* (S) ...	Small intestine.
	Dictyocaulus filaria (S)	Bronchi.
	Fasciola sp. (R)	Liver.
	Moniezia planissima sens lat. (R) (in Lamb)	—
	Cysticercus tenuicollis (S and R) ...	Mesentery.
	Echinococcus granulosus (hydatid cyst) (S and R)	Liver, lung, spleen.
PIGS... ...	*Metastrongylus* ? *apri* (S) ...	Bronchi.
	Œsophagostomum dentatum (S) ...	Large intestine.
	Cysticercus cellulosæ (R)	Musculature.

CARNIVORES.

Dog ...	*Spirocerca sanguinolenta* (R and S)	Perivascular connective tissue.
	(Syn. = *Spiroptera sanguinolenta*)	—
	Toxascaris leonina (S)	—
	Uncinaria stenocephala (S and R)	—
	Dipylidium caninum (S and R) ...	—
	Echinococcus granulosus (S and R) (Adult)	Intestine.
	Mesocestoides lineatus (S and R) ...	—
Cat ...	*Rictularia cahirensis* (S)	Intestine.
	" *Synthetostrongylus pusillus* " (R)	—
	Æleurostrongylus abstrusus (larvæ) (S)	Lung.
	Tænia crassicollis (R)	—
	**Tænia tæniæformis* (S)	—
	Dipylidium caninum (S) ...	—
	Joyeuxia chyzeri (S)	—
	**Mesocestoides lineatus* (S) ...	—
	Dithyridium elongatum (S) ...	Pleural and abdominal cavity and mesentery.
HEDGEHOG ...	*Prosthenorchis erinacei* (S) ...	Intestine.
	Cysticercus sp. (S)	Liver.
FOWL ...	*Subulura brumpti* (S)	Cæcum.
	Allodapa suctoria (R)	—
	Raillietina tetragona (R) ...	—

Note on the foregoing List.

In the case of those specimens marked with an asterisk, there is uncertainty as to the occurrence of the parasite in this particular host.

Those marked (R) are recorded in Dr. Roe's list (1929), those marked (S) are recorded for the first time, or from a new host, in the present paper. Those marked (S and R) are recorded by both Dr. Roe and the writer from the same host.

Note on the records of Human Parasites in Cyprus.

The only sources consulted are the Annual Reports of the Chief Medical Officer for Cyprus, issued between 1913 and 1924 inclusive. Each annual report records a large number of "parasites" from man, but does not go further. The only human parasitic infections for which specific diagnosis has been made are :—hydatid (47 cases) and *Tænia solium* (29 cases). There are also recorded 18 cases of "Tapeworm," of which 6 at least are presumably not *T. solium*, since they are recorded in a list in which that species figures elsewhere ; and nine cases of unspecified "roundworms." Fifteen cases of the removal of leeches from the naso-pharynx are recorded, but the leech is not specified.

(*Limnatis nilotica* Savigny is a well-known naso-pharyngeal semi-parasite of man in the Nile Valley, and may be the leech here mentioned.)

In the report which contains his list, Roe records heavy mortality and loss of produce due to parasitic gastro-enteritis and parasitic bronchitis in sheep and goats (p. 8). The following parasites mentioned in the above list might be associated with the gastro-enteritis condition in sheep and goats :—*Œsophagostomum venulosum*, *Trichuris ovis*, *Ostertagia circumcincta*, *Trichostrongylus vitrinus :* and the following with parasitic bronchitis :—*Dictyocaulus filaria*, a familiar cause of the disease, and *Protostrongylus ocreatus*.

None of the parasites recorded in either Dr. Roe's list or in this paper is new to Science or even particularly rare, and the record can only aim at being a contribution to our knowledge of the zoögeographical distribution of helminth parasites of domesticated animals in the Mediterranean sub-region. A few previous records, for this part of the world, of the parasites dealt with here are now appended.

Strongylus vulgaris and *S. edentatus* recorded for Egypt by Looss, 1901.

Trichostrongylus vitrinus, by the same author, for Egypt, 1905.

Gongylonema pulchrum recorded for Italy by Baylis, 1925.

Dictyocaulus filaria found by the writer in material from Palestine, 1931.

Subulura brumpti occurred in the same collection from Palestine. Also recorded for Spain and Algeria by Cram, 1927.

Rictularia cahirensis is known to occur in Egypt and Turkestan.

Cysticercus bovis, *C. tenuicollis*, *C. cellulosæ* and *Echinococcus granulosus* are all common parasites of live stock on the Palestine mainland, as shown by their abundant occurrence in material from there.

Joyeuxia chyzeri. Lopez Neyra records the cysticercoid of the worm (p. 438) from *Tarentola mauretanica* (Linn., 1758), a gecko which occurs in the Mediterranean lands from Spain to Egypt and is there preyed upon by cats.

Dithyridium elongatum. Blumberg's description probably refers to Russian specimens. He records it from both cat and dog. Cadéac records it from the Lyons and Toulouse districts of France. He associated the parasite with light peritoneal inflammation, broncho-pneumonia lesions and pyloric sarcoma in the cat.

Moniezia planissima is synonymous with *M. benedeni* (Moniez, 1829), and both this and *M. expansa* were found by the writer to occur in Palestine.

Trichonema catinatum is synonymous with *Cylichnostomum catinatum* (Looss, 1900), and is recorded by Looss from Egypt (1901, p. 128).

The remaining species are all cosmopolitan or well-known European parasites. As one would naturally suppose, the helminthic fauna of Cyprus shows a close approximation to that of Palestine and Egypt and Mediterranean Europe, whence the Cyprian fauna has probably been introduced.

The writer wishes to express his indebtedness to Professor R. T. Leiper, F.R.S., for placing the material here described at his disposal and for subsequent advice and assistance : and to Dr. T. W. M. Cameron for kindly identifying the larvæ of *Æleurostrongylus abstrusus*.

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Fig. I. × 130 diam.

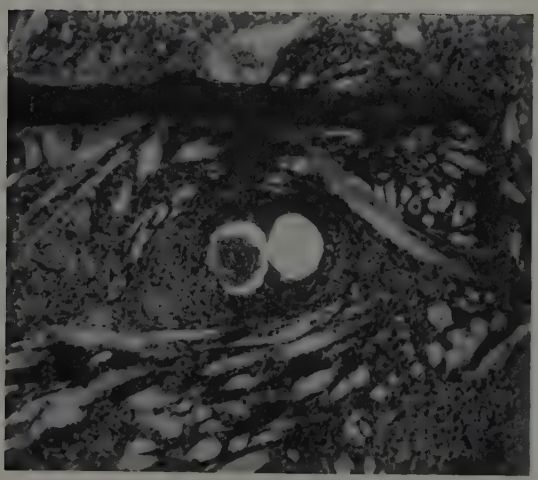

Fig. II. × 200 diam.

Sections of Habronema Nodules excised from the conjunctiva of a Mule.

[*To face p. 14.*]

Journal of Helminthology, Vol. x, *No.* 1, *February*, 1932, *pp.* 15-20.

Oxyuris stroma Linstow, 1884.

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Introduction.

It has been held for many years that the species of Syphacia found in the field mouse (*Apodemus sylvaticus*) and originally described by von Linstow (1884) under the name of *Oxyuris stroma* is the same as *Syphacia obvelata* (Rud., 1802)—a common parasite of rats and mice and occasionally found in man.

Seurat (1915) first expressed the opinion that these two species were identical, and later (1916) this author definitely placed *O. stroma* as a synonym of *S. obvelata*. Subsequent workers have accepted this view, although there does not appear to have been any detailed studies made of these two parasites.

It would appear, according to von Linstow, that both species occur in *A. sylvaticus* since this author (1879) has described and figured *S. obvelata* from this host as well as *O. stroma*. The differences between the two species are not very clearly brought out, and von Linstow's figure of the tail end of the male in *S. obvelata* is very similar to that found by the present writer in *O. stroma*.

The difficulty of making a detailed study of some of the species of Syphacia arises out of the fact that the males are very rarely found even when the females are present in abundance. It seems probable that the females are fertilized before reaching full size and that after impregnation the males die and are soon passed out.

Recently, the writer was able to examine a number of field mice which contained a large number of worms belonging to the genus Syphacia and among these a fair number of males were present. A study of these specimens shewed that the males, at least, possessed characteres which distinguished them from the males of *S. obvelata* from *Mus musculus*, and it was, therefore, evident that these worms, since the host is the same, could be regarded as being the same as von Linstow's species *O. stroma*.

This species should now be referred to as *Syphacia stroma* (Linst., 1884).

Description of *S. stroma*.

The mouth is surrounded by three distinct hyaline lips and leads into a short pharynx. The parenchyma underlying the lips shews three prominences which bear at least three papillæ. These papillæ are rather indistinct and the writer was unable to make out with certainty the two pairs of double papillæ and the one single pair which were observed by von Linstow on the three elevations.

The cuticle is transversely striated and shews a marked inflation at the head end. This inflation extends approximately to the level of the nerve ring. The œsophagus is almost cylindrical and is followed by a sub-spherical bulb which is separated from the œsophagus by a well-marked constriction; the bulb shews a valvular apparatus.

Female.—Although many of the female specimens examined were mature and contained eggs, they did not appear to be very old, while the majority were barely in the adult stage. The measurements which are given below may, therefore, be rather below the average for this species, and this may account for the differences between these measurements and those given by von Linstow.

The females measure from 3·40 mm. to 3·95 mm. in length with a width of 0·05 mm. at the head end. The width increases to 0·21 mm. in the region of the vulva and then the body gradually narrows to about 0·08 mm. at the anus.

The œsophagus, including the bulb, measures 0·43 mm. in length and 0·05 mm. in width in the pre-bulbar region, while the bulb itself is about 0·10 mm. in width. The excretory pore is situated a short distance behind the œsophageal bulb at about 0·65 mm. from the anterior end.

Behind the excretory pore but well in the anterior half of the body lies the vulva, its position varying from 0·72 mm. to 1·19 mm. from the head end; it opens by a short vagina into a broad muscular ovejector.

The tail gradually narrows from the anus and ends in a fairly sharp point; it measures about 0·49 mm.

The eggs are large and asymmetrical and measure 0·130 mm. to 0·143 mm. by 0·042 mm. to 0·052 mm.

Male.—The male is much smaller than the female and is rarely found except when an infection appears to be of recent origin.

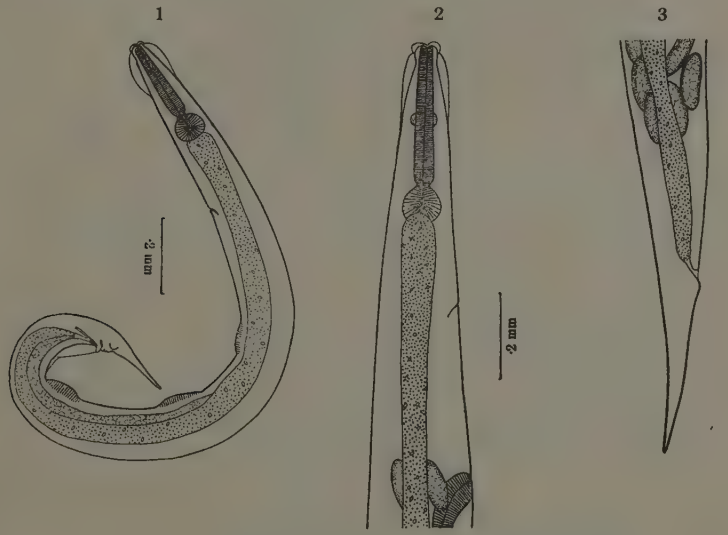

Fig. 1. Male of *S. stroma*, complete worm.
Fig. 2. Anterior end of female of *S. stroma*, lateral view.
Fig. 3. Tail end of female of *S. stroma*, lateral view.

The male varies in length from 1·74 mm. to 2·20 mm. with a maximum width of 0·15 mm. The œsophagus measures 0·29 mm., including the bulb, the latter being 0·07 mm. long and 0·066 mm. in width. The excretory pore is situated behind the œsophageal bulb at a point about 0·44 mm. from the anterior end.

The tail end is coiled and more particularly in those males which are shrivelled up and appear to be disintegrating. In these specimens also, the " mamelons " are usually very pronounced.

Caudal alæ are present and these are supported post-anally by two large papillæ. There are also present, near the cloaca, one pair of sessile ad-anal papillæ and one pair slightly pre-anal. The tail gradually

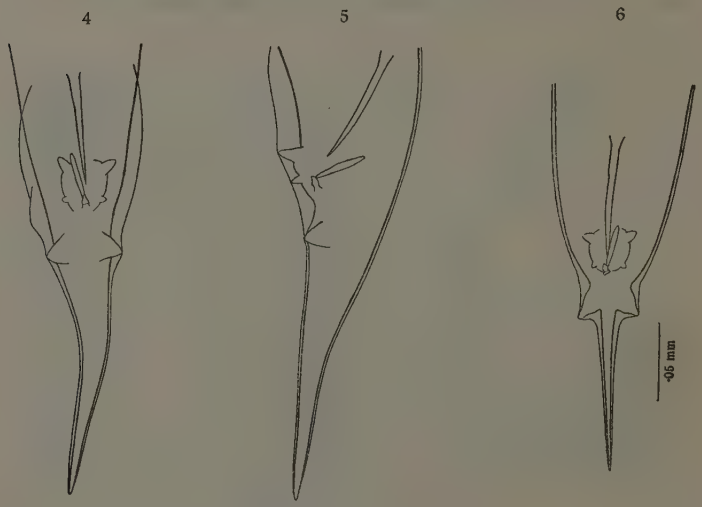

Fig. 4. Tail end of male of *S. stroma*, ventral view.
Fig. 5. Tail end of male of *S. stroma*, lateral view.
Fig. 6. Tail end of male of *S. obvelata*, ventral view.

narrows posteriorly and ends in a fairly sharp point ; it measures 0·18 mm. in length. Three cuticular " mamelons " are present on the ventral surface, the most posterior of these being 0·5 mm. from the tip of the tail. The anterior " mamelon " is less prominent than the other two and is situated in the anterior half of the body.

There is a single spicule present which is slightly curved and shews a slight constriction, when viewed ventrally, at about the anterior third of its length ; it measures 0·077 mm. in length. The gubernaculum is somewhat spindle-shaped and measures 0·03 mm. There is a chitinous hook on the posterior lip of the cloaca.

Remarks.

The measurements given in this paper for *S. stroma* differ in many instances from those given by von Linstow, but owing to the variations which occur in both this species and in *S. obvelata* one cannot attach too much importance to differences in size. Having regard to the fact that the host is the same, there appears to be, however, no reason for considering the species described above as being different from the one described by von Linstow.

As to the validity of *S. stroma* there is, at least in the male, a well defined character by which this species can be distinguished from *S. obvelata*. In *S. stroma* the tail narrows gradually from the region of the cloaca towards the tip (fig. 4), whereas in *S. obvelata* there is a far more pronounced constriction of the tail in front of the post-anal papillæ (fig. 6). These latter, when viewed ventrally in *S. obvelata*, appear as two large processes projecting well beyond the width of the body with the consequent outward stretching of the caudal alæ. The remainder of the tail, therefore, appears as a long narrow spine arising from the base of the post-anal papillæ. In *S. stroma* the papillæ, owing to the far more gradual narrowing of the tail, project very little beyond the width of the body in this region.

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Journal of Helminthology, Vol. x, No. 1, February, 1932, pp. 21-28.

On the Nomenclature of the Root-gall Nematodes.

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Introduction.

Nematodes belonging to two distinct genera are known as the causal organisms of galls on the roots of plants. One of these belongs to the genus Anguillulina=Tylenchus and the other to the genus Heterodera. The former, under the name of *Tylenchus hordei* Schøyen, 1885, has been known for many years as the producer of galls on the roots of certain grasses and cereals; the latter, under the name of *Heterodera radicicola* (Greeff, 1872) Müller, 1884, as the producer of galls on the roots of a very large number of wild and cultivated plants both monocotyledons and dicotyledons.

Amongst the numerous hosts of *H. radicicola* we generally find listed certain grasses including *Poa annua*, *Poa pratensis*, *Agropyron repens*= *Triticum repens* and *Elymus arenarius*. When we come to ascertain who first discovered and named the parasite on these hosts we find Greeff (1872) cited for *Poa annua* and *Agropyron repens*, Warming (1879) for *Elymus arenarius* and Henning (1898) for *Poa pratensis*.

Roots galls on *Elymus arenarius* are undoubtedly caused by the parasite generally known as *Tylenchus hordei* Schøyen, 1885. It was a matter of interest, therefore, to discover more about the original work of Greeff, including the nature of the galls and their causal organisms in the hosts attributed to him, particularly as the writer was aware from his own observations that both *Poa annua* and *Poa pratensis* are hosts of *T. hordei* also.

Pursuit of this enquiry led to the study of the early literature on the subject, including especially Greeff's original papers (1864 and 1872), in the second of which his *Anguillula radicicola* is first described, and the paper by Müller (1884) in which the name *Heterodera radicicola* is first used, as well as various other papers bearing on the subject. The upshot has been surprising in that it appears that Greeff's paper of 1872 which contains, under the name *Anguillula radicicola* an easily recognisable description of a Tylenchus species, was never seen by Müller who, nevertheless, took the specific name *radicicola* and applied it to *Heterodera*. In the following pages the relevant facts of the case are first set out, the matter is then discussed in the light of the International Rules of Zoological Nomenclature and finally certain recommendations are made concerning the necessary alterations in the names of the organisms.

Presentation of Data.

1. Greeff (1864) observed galls on the roots of certain unspecified grasses in the vicinity of Bonn, Germany, and found nematodes in them.

2. Greeff (1872) discovered nematodes in galls on the roots of a greenhouse plant, *Dodartia orientalis*, sent to him by Dr. Magnus from the Botanical Gardens, Berlin. He said that his observations had led him to the view that these nematodes agreed completely with those found, first by Schacht and later by himself, in the roots of plants.

These plants he gave as *Poa annua*, *Triticum repens* and certain unnamed species of Sedum. The worms, he said, are provided with a stylet-like mouth spear to enable them to penetrate the roots. He first considered that they belonged to the genus *Dorylaimus* Duj., but then decided to place them in the genus Anguillula under the name of *Anguillula radicicola*. He noted that they were different from the wheat eelworm, *Anguillula tritici* (*A. scandens*) and gave a description of them containing the following characters.

Female 2 mm. long by 0·095 mm. wide. Male rather smaller. Anterior end tapering somewhat and ending bluntly. Posterior end in both sexes pointed, the male having a pair of cuticular wings (bursa) enclosing the anus and spicules but not encircling the tip of the tail. The mouth is provided with a stylet-like spear lying in a cylindrical sheath, the hinder end being broad and furnished with three divergent knobs.

The cylindrical œsophagus ends in a muscular globular swelling lined internally with chitin. Then follows first a rather narrow region which soon becomes broader, leading to the intestine stretching backwards in the body and filled with fat globules. The female genital opening lies a little in front of the anus. The female gonad starts anteriorly in the region of the œsophageal bulb and after making one or two loops stretches backwards in the body to a short distance behind the genital opening. This part lying behind the vulva is a blind sac-like part of the uterus. The eggs lie in the anterior uterus mostly showing the first stage of segmentation. Behind the œsophageal bulb there is a short canal which opens on the surface of the body at the excretory pore. The remainder of the paper presents some general remarks on root galls observed at different times of the year and on the probable life-history of the worms and is not germane to our present purpose.

3. Braun (1875) gave a paper at the Berlin Natural History Society dealing with plant galls caused by nematodes and brought his communication to a close with a brief account of the root eelworm, *Anguillula radicicola* of Greeff. He did not reproduce Greeff's description of the parasites but pointed out that in structure and life-history they differ essentially from but are related to the worms first found by Schacht and later described by Schmidt under the name of *Heterodera schachtii*. The paper ends with some remarks on the economic importance of the sugar-beet nematode.

4. Warming (1879) found galls on the roots of *Elymus arenarius* in Denmark and attributed them to *Anguillula radicicola* Greeff.

5. Cornu (1879) described galls on the roots of sainfoin, *Onobrychis sativa*, found at Chateauneuf (Loiret) France. Within the galls he discovered nematodes giving rise to cysts, many of which contained an abundance of eggs. The cysts were in the cortex and sometimes in the vascular bundles of the roots. The outer membrane of the cysts, which was more or less held in the tissues, was yellowish brown in colour and sometimes projected towards the exterior. Cornu figured eggs and larva. He found similar gall-like swelling containing cystic worms on the roots of *Cissus aconitifolia* and *Clematis vitalba*. After discussing whether the parasite might be *Heterodera schachtii* Schmidt or *Anguillula radicicola* Greeff, he decided that rather than make a faulty identification

he would propose a new name for the parasite. This he did and gave it the name *Anguillula marioni* (nova. spec.).

6. Oerley (1880) transferred *Anguillula radicicola* Greeff to *Tylenchus radicicola.*

7. Müller (1884) published a long paper dealing with root galls from *Dodartia orientalis* and other plants. He first examined some of the dried roots of *Dodartia orientalis* from Dr. Magnus' herbarium and later had an opportunity of studying fresh galls on the same host. From these he described and figured the characteristically swollen females and the blunt-tailed males of Heterodera.

He stated that he had not seen Greeff's paper published in 1872 but had depended on Braun's account of it. He considered that as both Greeff and he had obtained nematodes from root galls on *Dodartia orientalis* he was justified in his belief that he had found Greeff's *Anguillula radicicola*,which he now showed to be a species of Heterodera. He therefore took the specific name *radicicola* and applied it to Heterodera, naming the worm *Heterodera radicicola* mihi.

A little further on in the paper he said that since Greeff had identified the producer of the galls in *Poa annua, Triticum repens* and Sedum species with that attacking *Dodartia orientalis*, he himself had no hesitation in recording these plants as hosts of his *Heterodera radicicola.* Still later, in discussing the systematic position of the parasite, he suggested that Greeff probably rejected Dorylaimus and chose Anguillula for its reception after he had found the swollen females and had decided that this genus was a suitably wide and embracing one in which to place it.

On p. 10, he stated that he had had an opportunity of examining some of Warming's material of *Elymus arenarius* showing root galls and these also he declared were caused by *Heterodera radicicola* mihi. It may be suggested in passing that this statement of Müller's as to the causal organism of root galls on *E. arenarius* was doubtless responsible for the opinion held by Frank and attacked by Schøyen that *H. radicicola* was the nematode concerned.

At the end of the paper, in summarising the chief features of the parasite, he calls it *Heterodera radicicola* (Greeff) Müller.

8. Schøyen (1885) gave a good account of the nematode causing galls on the roots of barley and *Elymus arenarius* in Norway and named it

Tylenchus hordei. He controverted the view that it was *Heterodera radicicola*. A few more facts concerning this parasite from *E. arenarius* may be set down here. Goodey (1925) gave a detailed description of it and besides showing that it was a distinct and valid species of Tylenchus, proved that the worms from *E. arenarius* could set up galls on the roots of barley and *Poa annua*.

9. Cobb (1890) in writing on the root-knot nematode spoke of it as *Tylenchus arenarius* Neal, but also used the name *Tylenchus* (*Heterodera*) *radicicola* Greeff.

Discussion.

Two principal questions arise for consideration and discussion from the foregoing data :—(1) the specific name of the parasite causing galls on the roots of *Poa annua, Poa pratensis, Elymus arenarius* and barley, at present called *Tylenchus hordei ;* (2) the validity of the specific name *radicicola* as applied to Heterodera.

1. In the International Rules of Zoological Nomenclature it is stated in Article 25, under the Law of Priority : " The valid name of a genus or species can be only that name under which it was first designated on the condition (*a*) that this name was pubished and accompanied by a indication or a definition or a description ; and (*b*) that the author has applied the principles of binary nomenclature.

Applying this to Greeff's account of *Anguillula radicicola*, we find that he satisfied condition (*b*) above in applying binary nomenclature and condition (*a*) in giving a description of the worms. This description is readily recognisable as that of a species of Tylenchus. Greeff doubtless considered that the worms from root galls on *Dodartia orentalis* and from galls on the roots of the grasses, *Poa annua* and *Triticum repens*, were one and the same, but it is clear, in the light of our present knowledge, that he actually described adult worms of both sexes from grass root-galls.

The size, 2 mm. long by 0·095 mm. wide ; the shape of the stylet and œsophagus, the position of the vulva a short distance in front of the anus, the disposition of the ovary with its two anterior loops, the presence of a post-vulval uterine sac and the caudal alæ in the male not surrounding the tip of the pointed tail ; all these show clearly that the parasite he was dealing with was really what was afterwards described and named *Tylenchus hordei* by Schøyen. The specific name *radicicola* which he gave to the parasite should therefore, according to Article 25, replace

the specific name *hordei*, since it was the first to be applied to members of this species which were at the same time recognisably described.

It has been shown in the data presented that Oerley (1880) transferred Greeff's *Anguillula radicicola* to *Tylenchus radicicola*. If now we adopt the findings of Baylis and Daubney (1926) who showed that the generic name *Anguillulina* Gervais & van Beneden, 1859, has priority over *Tylenchus* Bastian, 1865, as the name of the genus commonly called by the latter name, then the name of the species under consideration becomes :—*Anguillulina radicicola* (Greeff, 1872)

=*Tylenchus radicicola* (Greeff, 1872) Oerley, 1880.

nec *Tylenchus* (*Heterodera*) *radicicola* (Greeff, 1872) Cobb, 1890.

synonym *Tylenchus hordei* Schøyen, 1885.

2. With regard to the validity of the specific name *radicicola* as applied to Heterodera, it is clear that Müller, believing that the parasite, *Anguillula radicicola* Greeff, gave rise to galls on the roots of certain grasses and also on those of *Dodartia orientalis*, considered that he had found this species in the Dodartia material which he examined. He was throughout his work ignorant of or overlooked the fact that Greeff had described the worms and makes it clear, at least twice in his paper, that he had not seen Greeff's 1872 paper.

The specific name *radicicola* has been shown above to refer to a species of Anguillulina=Tylenchus and has been transferred to and used as the correct name for the parasite causing galls on *Poa annua*, *Poa pratensis*, *Elymus arenarius* and barley. The question now arises, can it still be used as the specific name for a member of the genus Heterodera ?

Article 31 of the International Rules of Zoological Nomenclature gives a ruling on this matter. It says :—" The division of a species into two or more restricted species is subject to the same rules as the division of a genus. But a specific name which undoubtedly rests upon an error of identification can not be retained for the misdetermined species even if the species in question are afterwards placed in different genera." Then follow illustrative examples.

This seems to fit the case under consideration exactly, for Müller, in ignorance, identified the parasites found by him with Greeff's *Anguillula radicicola* and used the specific name *radicicola* for his worms, calling them *Heterodera radicicola*. What he described undoubtedly belong to

the genus Heterodera, whereas we have shown above that what Greeff described belongs to the genus Anguillulina=Tylenchus. Article 31 makes it clear that the specific name cannot be retained for the misdetermined species, hence *radicicola* cannot be used with Heterodera in the sense employed by Müller.

This being the case it becomes necessary to find a new specific name for the root-knot nematode. A study of the literature shows that the parasite was named and described by Cornu in 1879 under the name of *Anguillula marioni* n. sp. His account reveals the fact that he had found within the gall-like swellings on the roots, first of sainfoin and then of *Cissus aconitifolia* and *Clematis vitalba*, the cyst-like bodies of the swollen female worms many of which were filled with eggs. The description is by no means full,but it is sufficient to show that he was dealing with the root-knot eelworm. For this reason Cornu's specific name, *marioni*, is taken as being the earliest available name for the parasite which accordingly becomes :—

Heterodera marioni (Cornu, 1879).
synonym *Heterodera radicicola* (Greeff, 1872) Müller, 1884.

Finally it may be suggested that the following grasses, *Agropyron repens*, *Elymus arenarius*, *Poa annua* and *Poa pratensis* should not be listed as hosts of the root-knot nematode, *Heterodera marioni*, until such time as further investigation has shown that they are capable of functioning as such.

Below are listed the plant-parasitic species of the genera *Anguillulina* Gervais & van Beneden, 1859 and *Heterodera* Schmidt, 1871.

Anguillulina species :—*Anguillulina agrostis* (Steinbuch, 1799), *A. alata* (Cobb, 1930) *A. angusta* (Butler, 1913), *A. arboricola* (Cobb, 1922), *A. balsamophila* (Thorne, 1926), *A. cancellata* (Cobb, 1925), *A. darbouxi* (Cotte, 1912), *A. dendrophila* (Marcinowski, 1909), *A. dipsaci* (Kühn, 1858) Gerv. & v. Ben., 1859, *A. dura* (Cobb, 1922), *A. fucicola* (de Man, 1892), *A. graminis* (Hardy, 1850), *A. mahogani* (Cobb, 1920), *A. millefolii* (Löw, 1874), *A. musicola* (Cobb, 1919), *A. pratensis* (de Man, 1881), Goffart, 1929, *A. radicicola* (Greeff, 1872), *A. similis* (Cobb, 1893), *A. sycobia* (Cotte, 1920), *A. tritici* (Steinbuch, 1799), Gerv. & v. Ben., 1859, type species.

It may be noted that although the three species, *A. alata*, *A. cancellata* and *A. dendrophila* are included in the list it is because they have been found associated with lesions in plant tissues; there is no evidence to show that they are causally related to these lesions.

Heterodera species:—*Heterodera punctata* Thorne, 1928, *H. marioni* (Cornu, 1879), *H. schachtii* Schmidt, 1871, type species.

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Journal of Helminthology, Vol. x, *No.* 1, *February*, 1932, *pp.* 29-32.

On a New Species of Oxyurid from the Grey Squirrel in Scotland.

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The grey squirrel (*Sciurus carolinensis*), although of comparatively recent introduction from North America, has become thoroughly acclimatised and may now be regarded as one of the native British Mammals. Comparatively little is known of its helminth parasites and the following oxyurid, found in the large intestine of a specimen shot in the north of Scotland, appears to be undescribed.

ENTEROBIUS, SCIURI sp. nov.

The male is 0·9 mm. to 1 mm. in length, while the female is 2·8 mm. to 3 mm. in length. The cuticle in both sexes is conspicuously striated. The anterior end in both sexes is similar in appearance. There is a cuticular swelling surrounding the mouth (Figs. 2 and 3) which is guarded by three small lips. The swelling is similar in all directions. The œsophagus is of the typical oxyurid type and measures about 0·22 mm. in both sexes, *i.e.* it is relatively much smaller in the female than in the male, being 1/13 and 1/5 of the body length in the female and male respectively. The nerve ring surrounds the constricted portion of the œsophagus and the excretory pore is situated posterior to the œsophageal-intestinal junction.

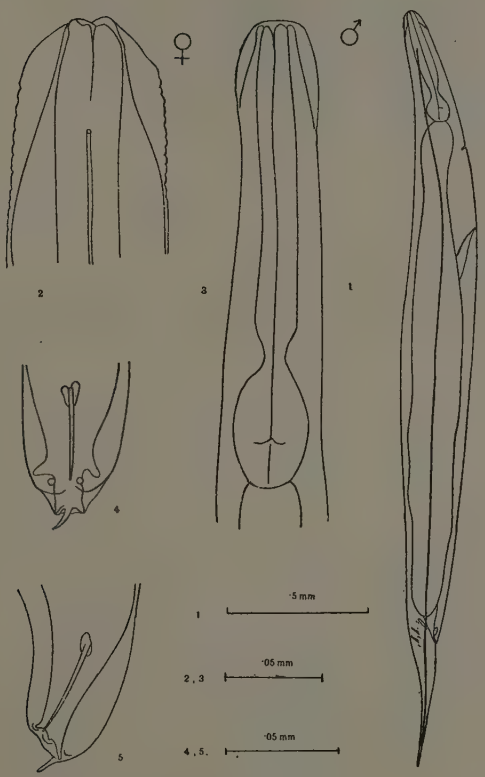
The male has a truncated posterior extremity with a small caudal spine. There are three pairs of anal papillæ, one pair situated on either side of this spine, and the other two pairs on either side of the ano-genital

opening (Figs. 4 and 5). All are small and inconspicuous. There is a single straight spicule, about 0·045 mm. long, with a double swelling at the anterior end. There is no accessory piece.

The female has a sharply pointed posterior end, the anus being situated 0·4 mm. from the tip (Fig. 1). The vulva is situated at the junction of the anterior and middle third of the body. It gives rise to a backwardly directed vagina which in turn communicates with opposed uteri. There are two refractile lateral crests present in the female which originate just behind the buccal swelling and terminate near the tip of the tail. These crests, although very obvious, do not project much beyond the surface of the cuticle; they are square in cross section. The ova are of the typical oxyurid type and have an average size of 50μ by 25μ.

Three species of Oxyuris (s.l.) are known from various species of Sciurus. *O. acutissima* of Zeder, from *S. vulgaris* is known only from the female which is imperfectly described. In any case, the female is 8·4 mm. long. *O. sciuri* from *S. atrodorsalis* is also known only from the female which is 17 mm. long. Both species are obviously different from the present form. *O. ungula* from *S. vulgaris* is more closely related. The male is 2·12 mm. long and the female 4·5 mm. long. The œsophagus is 1/5 of the body length in the case of the male and 1/7·5 in the case of the female. There are two caudal alæ. The male is not very satisfactorily described by von Linstow, but appears to terminate bluntly with two pairs of lateral projections; it is hoof-shaped when viewed from the side. No spicule was seen and the ano-genital opening appears to be some distance from the end of the body. The female has a small finely-pointed tail and the vulva is in the middle of the body. The eggs measure 120μ by 36μ. In spite of the inadequate description it seems obvious that von Linstow was not dealing with the present species.

This form does not fit easily into any of the existing genera of oxyurid worms. It appears to approach the genus *Enterobius* most closely. It differs from the described species in having only three pairs of anal papillæ in the male instead of four. The genus however contains forms which differ among themselves considerably—these differences being at least as great as those in the present species. Accordingly it is referred to the genus Enterobius with the specific name of *Enterobius sciuri* sp. nov.



Enterobius sciuri, sp. nov.

Fig. 1. Entire female.
Fig. 2. Lateral view of head of female.
Fig. 3. Lateral view of head of male.
Fig. 4. Ventral view of tail of male.
Fig. 5. Lateral view of tail of male.

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Journal of Helminthology, Vol. x, *No.* 1, *February*, 1932, *pp.* 33-44.

Some Observations on the biology of the Root-gall Nematode, *Anguillulina radicicola* (Greeff, 1872).

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Introduction.

In a paper published in 1925, the writer described the anatomy of the adults of this parasite and amplified Schøyen's account of it. At the same time it was shown that infective material derived from *Elymus arenarius* could give rise to galls on the roots of barley and *Poa annua*. Kemner (1930) has quite recently shown experimentally that the parasite from barley can set up galls on *E. arenarius* and presented important data on the agricultural significance of the parasite in northern Sweden. Detailed information as to which is infective stage of the parasite and on its life-history have so far been lacking and in order to remedy this omission the writer made a number of observations and carried out certain cultural experiments during 1927 and in the months of July, August and September 1931. These latter were made possible by the arrival during July of a good supply of galled roots of *Elymus arenarius* received in a living condition. The material came from sand dunes in the vicinity of Aberdeen and was collected by Dr. Alex. Smith of the Ministry of Agriculture Plant Pathological Laboratory, Harpenden, when away on vacation. The writer desires to express his gratitude and thanks

to Dr. Smith for his kindness in collecting and sending the material.

Larval Development.

Two lines of investigation were followed; one on very small and presumably young galls on the roots of *E. arenarius* and the other on galls on barley roots in experimental infections.

Dissection of large galls on *E. arenarius* directly the material was received yielded adults larvæ and eggs of the parasite. Several of the smallest larvæ were collected, killed by heat over a flame and measured. A number of embryonated eggs were also collected, placed in a shallow drop of water in a glass capsule and covered to prevent evaporation. As larvæ hatched from the eggs they were collected, killed and measured. By this means it was possible to recognise the first stage larvæ which were found to have a length of 0·42 mm. to 0·5 mm. and the following proportions:—α = 29-30, β = 7-4, γ = 7. These dimensions are rather larger than those given by Kemner for larvæ hatching from eggs whose figures are 0·3 mm. to 0·36 mm. long. It is clear that a good deal of variation in length is possible at this stage. The larvæ are slender and have tapering, rather sharply pointed tails. Stylet, œsophagus and intestine are typical and are readily recognisable, but the anus is often very indistinct. The genital primordium is found as a small clear area about halfway down the intestine.

Infective Stage. A very small gall on the tip of a rootlet of *E. arenarius* was carefully opened with needles in water and yielded one small larva measuring 0·49 mm. long. On the same day another very small gall yielded two larvæ measuring 0·46 mm., whilst still another gave two larvæ measuring 0·53 mm. It was clear from these observations that the infective stage of the parasite is the 1st stage larva which is capable of entering roots and of giving rise to galls.

Ecdyses. From the numerous galls dissected both on *E. arenarius* and on barley roots, experimentally infected, larvæ were obtained in various stages of development and undergoing ecdysis. They were mounted on slides in water and after being killed by heat were drawn in outline under the camera lucida so that their dimensions might be obtained.

1st ecdysis. This takes place when the larvæ have reached about 0·57 mm. to 0.59 mm. long. They have practically the same appearance as first stage larvæ.

2nd ecdysis. Growth in length and width takes place and this moult occurs when the larvæ measure from 0·65 mm. to 0·68 mm. long. The genital primordium has lengthened a little but is still found towards the middle of the body.

3rd ecdysis. This takes place in larvæ measuring 0·78 mm. to 0·8 mm. long. In these there is a more posterior extension of the developing gonad and the sexes are becoming just distinguishable from each other. The tails appear to have a rather different shape, the male tapering more suddenly than the female.

4th ecdysis. This is the last and is shown by worms measuring from 1 mm. to 1·3 mm. long in males and 1 mm. to 1·48 mm. long in females. The two sexes are now readily separable on the shape of the tail. In the male the developing spicules and bursal wings can be seen through the cuticle whilst in the female the vulva and the blind post-vulval uterine sac can be distinguished. In both sexes the gonad has grown posteriorly and linked up with the external opening.

Experimental Infections.

The material obtained from the dissected galls on *E. arenarius* provided a source of infection for experiments with barley seedlings.

1st experiment. Barley was sown in a Petri dish containing moist sand on July 14th, 1931, and at the same time a number of eggs and small larvæ of the parasite were added to the medium. Only one barley seedling was obtained as the grain used was a poor sample, but on July 20th the sand was carefully removed from around the roots of this seedling, which were then examined under the microscope in another dish of water. No galls had been produced on any of the roots at this time, but two small larvæ were observed in the vicinity of one root tip. The seedling was planted again in the same moist sand.

On July 31st the roots were again examined in water and three small galls were found at the tips of three long roots. One of these was cut off; it was a gall formed by the swollen root-tip which had bent back on itself and measured about 2 mm. long by 1 mm. wide. It was

carefully dissected with needles in a drop of water and from it about 50 larvæ were obtained. Many of these were killed by heat and then measured; some were about 0·46 mm. to 0·5 mm. long, *i.e.*, they were still in the first stage of growth, others measured 0·57 mm. long and showed the first ecdysis, whilst one measured 0·67 mm. long and showed signs of the second ecdysis.

The seedling was replanted in the same dish of sand and the roots were next examined on August 10th. It was soon seen that the galls had not increased in size so they were removed and dissected. One of them yielded a number of rather small larvæ which had developed but little beyond the stages seen 11 days previously. One, however, was larger than the rest and showed by the shape of the tail that it was a male almost ready to undergo the last ecdysis. The other gall yielded only two small worms. It seemed probable that the roots had been injured in being replanted in the dish of sand after the previous examination. The results may be summarised as follows:—After 6 days, no galls formed but larvæ seen close to root-tip; after 17 days, galls formed on roots, some of the infective larvæ still in the first stage of growth, others showing 1st and 2nd ecdysis; after 27 days, one worm almost adult.

2nd experiment. On July 23rd, barley was shown in soil in an observation box with a sloping glass side on to which the roots would descend in the course of their growth. A sheet of tin was arranged against the outside of the glass to exclude light. Several large galls from the roots of *E. arenarius* were broken up and mixed with soil where the seed was sown. The latter germinated well and seedlings were showing above ground in 4 or 5 days.

On August 17th, 25 days from the beginning of the experiment, the roots were examined through the glass and galls were seen to be present. Some of the soil was carefully removed and two galls were cut off, washed in water and dissected. One of them contained only two worms, one of which was damaged in opening the gall. The other contained 4 worms—1 adult male and 3 females not quite adult. One of these was undergoing the final moult and the other two showed the position of the vulva. The male was 1 mm. long and had the following proportions:—$\alpha = 35{\cdot}4$, $\beta = 7{\cdot}1$, $\gamma = 9{\cdot}3$; the females were each about 0·88 mm. to 0·9 mm. long.

This result agrees very well with the first experiment in which an almost adult worm was found at 27 days from the commencement of the experiment. If we deduct 6 to 7 days to allow for root development, since it was found in the first experiment that no galls were present after 6 days, we can safely assume that development from the 1st stage larva to the adult condition takes about 18 to 21 days.

On August 31st, after 39 days, 3 more galls were removed from the roots and dissected. One of these contained 2 adult males, 2 adult females and 1 immature male. The second contained 6 large males, and 6 large females as well as many free eggs, whilst the third contained 10 or more males and the same number of females as well as many free eggs.

On September 17th, 56 days from the beginning of the experiment, a barley plant was dug up and after washing the roots, 3 galls were cut off and dissected. In each, up to 5 or 6 large adults of each sex were found as well as many free eggs in an embryonated condition, but no larvæ were present. Four spiral-shaped galls were examined and found to be disintegrating ; they contained no worms or eggs.

Galls dissected on September 25th, *i.e.*, after 64 days showed large adults, many free eggs and some 1st stage larvæ. One large gall had completely broken down and contained no examples of the parasite.

Life History.

From the foregoing observations and experiments the course of the life history of the parasite may be taken to be practically as follows. First stage larvæ invade the roots and quickly give rise to galls in which they grow, undergoing four moults and becoming young adults in about 18 to 21 days. Growth and maturation of the gonads takes place and, after mating, egg laying begins in about another 10 to 12 days and continues for many more days since eggs only and no free larvæ were found in galls 56 days from the beginning of the experiment. Larvæ were present after 64 days.

Since the 1st stage larva is the infective stage we may infer that with the production of embryonated eggs or 1st stage larvæ within the gall the normal course of the life-cycle is completed, as with the breakdown of the gall, eggs and larvæ will be set free and the latter will be able to

attack other roots. The fact that some galls were found disorganised on barley roots after 56 and 64 days from the start of the second infection experiment shows that breakdown can be comparatively rapid.

It is not clear, however, whether this is the whole story for the question has presented itself of whether a second generation of adult parasites can arise within one and the same gall. It was found in the dissection of some of the large galls on the roots of *E. arenarius* in July that there were present large adults, very many eggs, many 1st stage larvæ and, in addition, intermediate developing larvæ in various stages of growth, some in the last ecdysis.

It is impossible to decide from observations of this kind whether these almost adult individuals belong to a second generation or if they are in a delayed state of development. In the same way, in seeking further light on this point, galls on rye seedling roots were examined. These had been lifted and fixed in formalin 80 days from the beginning of an infection experiment carried out in 1927. One of these large galls when opened contained many full grown adults, large numbers of eggs and 1st stage larvæ, several small adults and some late larvæ in an almost adult condition. These also might have belonged to a second generation or have been members of the invading generation suffering a delayed development.

From the fact that the 1st stage larva is the infective stage, that galls have been found disorganised after 56 days and that most large galls contain a far larger proportion of eggs and 1st stage larvæ than later larvæ, the writer concludes that one generation of the parasite per gall is the normal course of events. At the same time the possibility of a second generation per gall must be reckoned with and cannot be ruled out. This may depend on the internal state of the gall, *i.e.*, whether it is in a fairly stable condition or whether there is a plentiful supply of food. At the present time, however, no evidence is available on these latter aspects of the question.

Quiescence and Reviviscence.

Trail (1881) stated that the worms from the galls on *E. arenarius* roots were able to endure desiccation without being killed but he had not had an opportunity of testing this power over a long period.

Thomson (1928) says " the larvæ survive, as we have verified, for a couple of years the dryness of a shelf above steam heating pipes. After two years of this drought they moved about soon after the galls, soaked in water, were teased out."

From neither of these statements is it clear whether adults can survive as well as larvæ nor whether larvæ in all stages of development can be revived after drying within the gall. In order to test the matter the writer removed galled roots of *E. arenarius* on their arrival in July and placed them in moist sand in a Petri dish. This was covered with a lid in such a way that moisture could slowly evaporate from the sand and the roots. The latter were not examined until the end of August, by which time the sand and the galls had been dry for 5 weeks. Two galls were then put in water and within a few hours had swollen up to their original size. One was opened after soaking for 5 hours and the other after 24 hours. In both, only the small first stage larvæ showed any sign of movement ; full grown adults and some intermediate stages remained quite motionless even after several days and finally disintegrated. Later soakings of other dried galls gave the same results ; only 1st stage larvæ exhibiting the power of revival and showing motility.

Gall Formation—Pathology.

Galls usually occur at the root-tip in the form of oval or roundish swellings and frequently cause the root to bend back on itself in a spiral curve. They vary much in size from about 0·3 mm. to 0·5 mm. in length and breadth to as much as 5 mm. to 6 mm. in length by 3 mm. to 5 mm. in width. Occasionally two or three galls are found close together. Large galls are also often found at some distance from the root tip and here the root may also exhibit a spiral twist upon itself.

Trail (1881) described the appearance of a transverse section of a normal root and contrasted it with that of a gall. The writer has also prepared transverse sections of normal roots and galls from *E. arenarius* and wheat and from an examination of these is able to confirm Trail's brief account.

A transverse section of a normal root of *E. arenarius* shows the following features (fig. 1). An outermost layer of mainly empty cells composing the epidermis from which root-hairs arise. Separating the epidermis

from the central vascular cylinder is the cortex, made up of 4 to 5 layers of regular thin-walled cells; those towards the centre being smaller and narrower and having slightly thicker walls than the middle ones. These again are a little larger than those next to the epidermis. The cortical cells contain but little protoplasm. The central vascular cylinder is surrounded by an endodermis, the cells composing which have their inner and lateral walls markedly thickened. Within the cylinder the constituent cells are very small.

A transverse section of a gall (a portion of one is shown in fig. 2) shows that the epidermis is not materially altered except that root-hairs are absent and the individual cells are larger than normal. The cortex is very greatly altered, being now composed of 10 to 12 layers of large cells. The inner ones are again smaller than the median and outer ones and for the most part are full of granular protoplasm. Many cells show a large nucleus containing two or more prominent nucleoli. Collapse and breakdown of some of the cortical cells takes place giving rise to large cavities in which the parasites occur. The central cylinder is also greatly affected by the parasite, being much enlarged and frequently showing a width almost equal to that of an entire transverse section of a normal root. The individual cells composing it and the endodermal layer are also of much greater size. There is much more granular protoplasm present within the cylinder than in the normal root. The endodermis too shows signs of progressive loss of the thickening of its inner and lateral walls as indicated in the cells on the left of the central cylinder in fig. 2. Where these thickenings have gone the lateral walls break down and some of the sections examined by the writer coming from the central part of a gall showed the whole endodermis without thickenings on its walls and all the lateral walls broken. Such an internal condition must gradually lead to the disruption of the entire gall. Wheat roots also exhibited the same great increase in size and numbers of the cortical cells and marked enlargement of the vascular cylinder as compared with the normal root though the details of structure are different and the endodermis is not so heavily thickened as in *E. arenarius* roots.

On breaking galls open in water the parasites are easily floated out from the fairly large cavities found within the cortex. As far as observation of teased-up galls and sections shows, the parasites do not appear

to puncture the enlarged cortical cells and it must be assumed that they feed on substances poured out from these cells into the intercellular spaces. The enlarged and richly granular cortical cells seem to be analogous to the giant cells produced in other plant galls caused by insects and nematodes.

Fig. 1. Transverse section of a normal root of *Elymus arenarius*.
Fig. 2. Portion of transverse section of a gall on a root of *Elymus arenarius* drawn to the same scale as fig. 1.

Kostoff & Kendall (1930) have recently investigated and discussed in a very interesting manner the formation of giant cells in the roots of *Nicotiana* plants under the attack of the root-knot nematode, *Heterodera marioni=H. radicicola*. They point out that plant tissues exhibit an increased permeability and exosmosis under the influence of toxic substances and suggest that the parasite pours out some toxic

secretion from its œsophageal (salivary) glands in response to which the permeability of the cells is increased and an accumulation of nutrients results in the region attacked. This accumulation of food substances leads to increased and accelerated cell growth in the affected part and results in a localised swelling or gall.

The parasites feed on the nutrients exosmosed from the enlarged highly granular cells which arise as a result of their presence and the host plant suffers in that nutriment which should be translocated and used in the building of other organs is localised in the galls ; growth and health of the plant are consequently adversely affected.

This view of the process of gall formation may equally well apply to the conditions met with in *E. arenarius* and other hosts of *Anguillulina radicicola*. The response of the plant to the presence of only one or two larvæ of the parasite is most remarkable ; resulting as it does in the alteration and enlargement of a large number of cortical and vascular cells many of which occur at comparatively long distances from the location of the parasite. The whole aspect of the structure and internal arrangement of the gall is suggestive of the action of a diffusible toxic principle rather than the attack of an organism, by puncturing, etc., on individual cells.

Hosts.

Greeff found the parasite in root galls on the annual meadow-grass (*Poa annua*) and couch grass (*Agropyron repens*), Warming and Trail on sea lyme grass (*Elymus arenarius*), Eriksson & Schøyen on barley (*Hordeum sativum*), Henning and Rostrup on smooth-stalked meadow-grass (*Poa pratensis*), a host on which it was also found early in 1930 on plants coming from Derbyshire.

The writer confirmed the occurrence of galls on barley and *Poa annua* in 1925 and showed that they could be set up by infective material from *E. arenarius*. A further series of infection experiments was carried out during 1927 when seeds of various cereals and grasses were sown in pots the soil of which contained infective material from galls on the roots of *E. arenarius*. The experiment ran for 80 days when examination of the roots showed galls on the following :—wheat, rye, oats, *Arrhenatherum avenaceum* and *Aira flexuosa*. The galls on wheat and

rye were abundant and large,whereas on oats and the two grasses there were only one or two galls containing rather smaller adult worms and from this it was concluded that although susceptible to attack, these hosts are not so favourable to the parasite as barley, wheat, and rye. At the same time the following grasses were tested and found to be free from galls :—*Dactylis glomerata, Anthoxanthum odoratum, Cynosurus cristatus, Poa pratensis, Festuca ovina, Phleum pratense, Agrostis stolonifera, Lolium perenne* and *Lolium italicum.* It will be noticed that *Poa pratensis* failed to show galls whereas it is known as a natural host in Sweden, Denmark and England.

Botanical Name.	*Common Name.*	*Earliest Recorder.*	*Countries.*	*Remarks.*
Agropyron repens = *Triticum repens*	Couch grass ...	Greeff, 1872 ...	Germany... ...	Nat. Inf.
Aira flexuosa	Wavy hair grass	Goodey ...	England	Exptl. Inf.
Alopecurus pratensis ...	Meadow fox tail	Hellström, 1917	Sweden	Nat. Inf.
Arrhenatherum avenaceum = *Avena elatior*	Tall oat grass ...	Goodey ...	England	Exptl. Inf.
Avena sativa	Oats	Kemner, 1930,	Sweden	Exptl. Inf.
		Also Goodey ...	England	Exptl. Inf.
Elymus arenarius ...	Sea lyme grass	Warming, 1879	Denmark, Sweden Norway, Scotland	Nat. Inf.
Hordeum sativum ...	Barley ...	Eriksson, 1885	Sweden, Norway, Finland	Nat. Inf.
Phleum pratense ...	Timothy ...	Hellström, 1917	Sweden	Nat. Inf.
Poa annua	Annual meadow-grass	Greeff, 1872 ...	Germany... ...	Nat. Inf.
			England	Exptl. Inf.
Poa pratensis	Smooth-stalked meadow-grass	Henning, 1898	Sweden, Denmark, England	Nat. Inf.
Secale cereale	Rye	Hellström, 1917	Sweden	Nat. Inf.
			England	Exptl. Inf.
Triticum vulgare... ...	Wheat ...	Goodey ...	England	Exptl. Inf.

It should be remembered that the infective material came from *E. arenarius* whereas under natural conditions, it is conceivable that *Poa pratensis* may have its own specially adapted strain of the parasite. Again, too much weight should not be attached to this single negative result from a small pot experiment as still further work is needed on the host reactions of this parasite. This is shown from the work of Kemner (1930), who points out that Hellström (1917) found rye, *Alopecurus pratensis* and *Phleum pratense* attacked in northern Sweden whilst Kemner himself was unable to get galls formed on the roots of *Phleum pratense* when using infective material from *E. arenarius.* Both *Phleum pratense* and *Festuca ovina* were smaller, however, than when grown in normal soil.

The list on the preceding page includes those hosts which have been found harbouring the parasite under natural conditions and those in which galls have been produced under experimental conditions.

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Journal of Helminthology, Vol. x, *No.* 1, *February*, 1932, *pp.* 45-52.

On a New Parasitic Protozoon associated with a Sickness in a Bilharzian Intermediate Host.

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During a recent expedition carried out by Dr. W. K. Blackie and Mr. W. A. McDonald in Southern Rhodesia, large numbers of the snail *Bulinus tropicus* were collected for living storage in aquarium tanks in the Medical Zoology Division of the London School of Hygiene and Tropical Medicine. They were collected about the 20th February, 1931 and were brought to London on the 30th March and were distributed amongst several separate tanks. Some five weeks later some of the snails were overtaken by a curious sickness which gradually but rapidly spread to the rest and within a fortnight of their first appearance, the characteristic symptoms were present to a greater or less degree in almost every one of the snails, which numbered several hundreds. The sickness proved fatal in many cases and towards the end of three weeks the mortality was nearly 50 per cent. Thus it appeared likely that the whole collection would eventually be destroyed when the epidemic, as it seemed to be, spent itself with surprising suddenness and the remaining snails made a rapid recovery.

The possibility having been considered, amongst many others, that the sickness was caused by some parasitic infection, press preparations were made of the organs and tissues of dead snails, which led to the finding of the parasite described herein. A high percentage were thus examined

and with very few exceptions, the infection was found to be present and a similar result was obtained on the examination of sick and dying snails, though only a few of these could be sacrificed for this purpose.

Whether the sickness was caused by this parasite or whether it was due to an unsuitable physical environment or to some other cause altogether, has yet to be definitely ascertained. Should the former prove to be the case, then it would be a fact of more than academic interest, inasmuch as the possibility suggests itself that in the natural habitat the protozoa may act as a biological control on the snails.

Morphology.

The oöcysts, which were spherical or subspherical, and ranged in size from 70μ to 112μ diameter, possessed a hyaline double-contoured wall of 0·8μ to 1μ in thickness. No indication of a micropyle could be detected, but as it was impossible to separate the oöcyst completely from the tissues of the host owing to the tendency of the oöcyst wall to rupture under the slightest pressure, the possible presence of a micropyle could not be definitely excluded.

The contents of the oöcysts were in every case fully differentiated into sporocysts, and no residual cytoplasm was present. The number of sporocysts contained by the oöcysts showed the wide range of from 18 to 42 although individuals containing less than 26 or more than 32 sporocysts were comparatively rare. A peculiar and striking feature of the sporocysts was that each was provided with an individual casing or envelope of a colourless, transparent, jelly-like substance. This was most apparent in fresh cysts newly dissected from the host, when the outlines of the casings could be clearly seen forming rounded contours towards the outside of the mass where space existed between the mass of sporocysts and the oöcyst wall, and giving a honeycombed appearance towards the centre where the sporocysts were in closer apposition to one another, and the jelly-like casings were compressed together. When partially dissected-out oöcysts were kept in a moist chamber for a few days, these outlines gradually faded and disappeared although the spacing of the sporocysts remained the same, suggesting that the casings had merged together rather than disappeared. The sporocysts were somewhat lemon-shaped, but with one side slightly flattened. The

wall was distinct and double-contoured, about 0·6μ in thickness. At one end a nipple-like projection occurred, and at this point the wall was pierced by an orifice which was closed by a clearly outlined plug of a slightly greenish, highly refractile substance. When sporocysts were freed from the oöcyst by the rupture of the latter, in very fresh material a prolongation of this plug extending through the jelly-like casing could frequently be made out. Distally this prolongation either terminated abruptly, or, more usually, merged imperceptibly into the substance of the casing.

The dimensions of the sporocysts showed comparatively slight variations, and the range of variation was as great among individuals contained by a single oöcyst as among individuals from different oöcysts taken from different hosts. In length the sporocysts varied from 16·6μ to 19μ and in greatest thickness from 12·3μ to 16μ.

The contents of the sporocysts which were obtained from the first snails to be dissected were undifferentiated, consisting of a mass of granular cytoplasm completely filling the internal cavity. In some cases a spherical vesicular nucleus with large central karyosome could be made out, while rod-like bodies, similar in appearance to the chromatoid bodies in the cysts of *E. histolytica* were occasionally present in the cytoplasm.

After being kept in a moist chamber for two days, the contents of these sporocysts were found to round up into a more or less centrally placed spherical mass. Sporozoite formation then began to take place but in more than 90 per cent. of the sporocysts this process was not completed but was interrupted by degenerative changes, the cytoplasm gradually breaking down into several small masses which became scattered irregularly through the cavity of the sporocyst. This occurrence was no doubt due to the degeneration changes taking place in the host tissue which could not be completely eliminated from the cultures. The addition of chemical solutions, such as chromic acid, to the cultures, was found to be useless as a means of checking decomposition, since in every case the substance added penetrated both oöcyst and sporocyst walls and caused the death of the parasite. Under the artificial conditions of the moist chamber, a period of from 14 to 20 days was necessary for the development of the sporozoites to be completed.

Three months after the first discovery of the parasite the infected snails which were dissected showed only a few oöcysts, and, on examination, the contained sporocysts were found in every case to show a late stage of sporozoite formation. A single sporozoite was contained in each sporocyst and no residual cytoplasm could be distinguished. The sporozoites were elongated, club-shaped organisms with the thick end containing a spherical vesicular nucleus with large central karyosome, and in some instances a vacuole in the cytoplasm adjacent to the nucleus.

Fig. 1.—Oöcyst containing sporocysts with undifferentiated contents. (X 600 approx.)

Figs. 2 & 3.—Sporocysts with fully developed sporozoites. (X 1150 approx.)

Figs. 4 & 5.—Sporocysts, containing fully developed sporozoites, showing internal membrane and stalk-like prolongation of plug extending into outer jelly-like casing. (X 1150 approx.)

This end was constantly arranged towards the opening in the sporozoite wall. The narrow end of the sporozoite was recurved and bent upon itself in a variety of ways.

In both size and shape the sporozoites showed slight differences. In length they varied from 30μ to 37μ, the greatest width varied from 6·5μ to 9μ, and the degree to which the body tapered showed a corresponding variation.

In some cases a very fine membrane internal to the sporocyst wall could be distinguished. This was usually fairly closely applied to the sporozoite and could be most easily seen at the anterior end of the latter where it extended across the dividing space to meet the plug-like structure which closed the anterior pore of the sporocyst. No indications of a bivalvular structure of either the sporocyst wall or the internal membrane, such as that shown by Schneider to exist in *Barrouxia ornata*, could be detected. The exertion of considerable pressure was necessary to effect any rupture of the sporocyst wall, and when this occurred it took the form of a lateral slit more or less perpendicular to the longitudinal axis.

Snails known to be infected with the parasite were sectioned in an attempt to discover other stages in the life cycle, but these attempts were unsuccessful. The sections showed, however, that the oöcysts were constantly lodged in a very loose connective tissue immediately subjacent to the outer epithelial layer of the mantle.

The Sickness and Its Cure. Feeding Experiments.

The first obvious symptoms of the sickness to be observed were a marked sluggishness accompanied by indifference to food. A day or two later the mobility of the snail, especially in the foot, was greatly diminished and gave rise to what was a very characteristic phase in the sickness. Thus, snails sick for two or three days, were seen to be lying at the bottom of the tank in an inverted position, with the foot uppermost and the dorsal side of the shell in contact with the tank. A healthy snail, if placed in this position, could regain the normal position within a few seconds by extending the foot dorsally and getting a grip with it on the surface of the tank. This, the sick snail was quite unable to do, the foot having apparently lost its extensibility and being capable only of rather feeble motions. Furthermore, even if placed in the normal position, the snail in many cases was unable to retain it and a very slight disturbance of the water sufficed to cause it to resume the inverted position. The next marked phase in the sickness was a swelling of the parts of the body outside the shell, and an extrusion and swelling of the mantle, so that its edge was reflexed back over the margin of the shell mouth. The " horns " at this stage were much retracted, with a flabby and lifeless appearance, and were almost insensitive. The foot, body and mantle also showed little of the normal quick reactions to tactile stimuli,

and if prodded with a needle withdrew only a little inside the shell. The colour of the body at this stage had changed considerably. Normally, an opaque dark greenish grey colour, the flesh had now a translucent pale yellowish appearance, and was not infrequently tinged with red, as though suffused with blood. This œdematous condition lasted for a day or two after which the swelling subsided and the snail retired within the shell, showing little evidence of life beyond a slight movement on being prodded with a needle. Ciliary action became much abated with the result that bits of débris adhered to the sides and sole of the foot, and on the surface of the shell, normally perfectly clean, a fungal growth appeared. Death generally ensued between the seventh and tenth day.

The sudden disappearance of the sickness, alluded to above, followed shortly after the snails had been transferred to a different medium. Previously, ordinary tap water had been used, which was aerated by a continuous stream from the main compressed air supply, a method of storage which has proved satisfactory over a long period in the case of other snails, notably species of *Planorbis*. At Professor Leiper's suggestion, pond-water with a high content of green algæ was obtained and the snails were transferred to this after being immersed for half-an-hour in a 1 in 500,000 solution of chlorine. The following day a marked improvement in their condition was noted and in another two days almost all traces of the sickness had gone.

There can be little doubt but that this treatment contributed largely towards the cure of the sickness, if indeed it was not solely responsible for it.

Acting on the assumption that the transmission of the protozoon parasite involved the ingestion by one snail of the parasitised tissues of another snail (for *Bulinus tropicus* has been observed to feed upon the dead bodies of its kind), an attempt was made to test the theory that the sickness was caused by an active phase in the life cycle of the parasite, and by feeding the oöcysts to healthy snails, to reproduce the sickness in them again. Several *Bulinus*, now completely recovered, and a single *Planorbis*, were accordingly fed with the oöcysts dissected from the tissues or with small pieces of tissue in which they were embedded. There resulted, however, no recurrence of the sickness in any of the snails thus fed. Furthermore, the sickness has not reappeared amongst

any of the surviving snails and this fact can hardly be attributed to any scarcity of infective material. In view of the fact, however, that the snails may have become immune to further infection, three young snails of a new generation bred in the laboratory from the survivors, were fed with oöcysts, but up to a month later, they showed no symptoms, nor was any stage of the protozoon found in them. It is of interest to note that amongst this new generation of *Bulinus*, there have been five isolated cases of sickness, but these showed no infection with the parasite.

The evidence, such as it is, is therefore somewhat conflicting, and the origin of the sickness remains for the present a matter for conjecture.

Systematic Position and Nomenclature.

Although only the final stage of the life cycle of this parasite is known, the well defined characters of the oöcysts, sporocysts and sporozoites are considered to give sufficient data for identification purposes.

The characters of the oöcysts are such as to justify the placing of the organism in the Sub-Order Eimeriidea of the Coccidiida, while the numerous monozoic sporocysts contained by the oöcyst are characteristic of the Sub-Family Barrouxinæ of the Family Eimeriidæ. Of the two genera included in this Family, only one, *Barrouxia* Schneider, 1885, possesses a smooth outer wall to the oöcyst. Five species of *Barrouxia* of which *B. ornata* Schneider, 1885, is the type, have been recorded, but none of these shows an exact morphological correspondence with the parasite described above, and none has been found parasitic in a mollusc *B. schneideri* (Bütschli 1882) Léger 1897, *B. legeri*, Schellack and Reichenow 1913, and *B. caudata* Léger, 1898 are parasitic in *Lithobius forficatus*, *L. impressus* and *L. martini* respectively, while *B. spiralis* Awerinzew, 1909 was described from a worm (*Cerebratulus* sp.) and *B. ornata* from the water scorpion *Nepa cinerea*. Of these, *B. ornata* most closely resembles the species described above in general morphological characters. It differs, however, from the latter in the size of the oöcyst and sporocyst and in the shape of sporocyst and sporozoite. Schneider gives the size of the oöcyst of *B. ornata* as only 34μ to 37μ diameter—rather less than half the size of the species in the snail, while the sporocysts of *B. ornata* measured from 10μ to 20μ in length, were pointed at either end and split longitudinally into two valves to liberate

the sporozoites. It is therefore concluded that the species from the snail is new to science and the name *Barrouxia bulini* is suggested for it with the following diagnostic characters :—oöcyst spherical to subspherical, 70μ to 112μ diameter. Sporocysts varying in number from 18 to 42, ovoid with nipple-like projection containing orifice closed by hyaline plug. A single club-shaped sporozoite contained by each sporocyst. No residual cytoplasm in oöcyst or sporocyst.

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IMPERIAL BUREAU OF AGRICULTURAL PARASITOLOGY.

NOTES AND MEMORANDA.

No. 5.

Differential Diagnosis of Plant-parasitic Eelworms.

In a circular issued early last year to the correspondents of the Bureau it was stated that: "It is unfortunate that there are no up-to-date text-books in English adequately covering the plant-parasitic eelworms, so that it becomes necessary to rely on a variety of key-descriptions which have appeared from time to time in the periodical literature." Since that circular was issued we have received letters from correspondents requesting us to issue references to these key-descriptions, and, in some cases, asking us to provide information sufficient for agricultural officers to identify the eelworms they meet with in their crops.

Quite recently there have been important and extensive changes made in the nomenclature of the plant-parasitic eelworms, and we are taking this opportunity of acquainting our correspondents with these new names. Manifestly, it will be convenient to deal with the changes in nomenclature first.

Nomenclature.

In order to avoid confusion and misunderstanding among systematists there is in operation a code of International Rules of Zoological Nomenclature designed to avoid ambiguity in the use of scientific names and to ensure uniformity by granting priority, in most cases, to the earliest of any group of synonyms. These rules generally operate smoothly and efficiently to the advantage of all concerned, but occasionally it is found by bibliographical research or by some new morphological discovery that an old and well-established name is not valid according to the Rules.

This involves a readjustment of scientific names which can be very annoying to the practical man, whose only interest in nomenclature is to find an unambiguous label to attach to the creatures which come under his notice. In the present case readjustments have been made in each of the three chief genera of plant-parasitic eelworms : *Aphelenchus*, *Heterodera* and *Tylenchus :* in fact, the only plant parasites among them which completely retain their old names are *Heterodera schachtii* Schmidt and *Heterodera punctata* Thorne.

It is quite probable that the older names will continue in use among practical men, at least for some time, but the importance of circulating this new information as early as possible lies in the fact that the new names will, from now onwards, be appearing in the scientific literature ; and failing a knowledge of these changes it is more than probable that an agricultural officer would be at a loss to recognize, say, *Anguillulina radicicola.*

The proposed changes will now be explained, taking each genus separately into consideration and giving very briefly the reason for the changes. Those who may wish to enquire further into this irritating subject should consult the papers mentioned in the following explanation, the full references to these papers appearing at the end of the memorandum.

APHELENCHUS.

An author who creates a genus is expected to designate one of the contained species as a type of that genus. If any of the other species are subsequently found to differ so greatly from the type that they cannot be considered congeneric, then they are removed from that genus ; but obviously the type species cannot be removed. Now the genus *Aphelenchus* was created by Bastian in 1865, but no species was designated as type in that paper. Bastian, however, subsequently (and unfortunately) designated *A. avenæ* as type in a letter to Stiles. This was unfortunate because the male of *A. avenæ* was then undiscovered, whereas other species were available in which the male was known and in these males no lateral caudal wings are present. Now, however, the males of *A. avenæ* have been discovered and they have a well-developed bursa, with ribs, similar to that of *Rhabditis* spp. It has been pointed out by Steiner (1931A) that all the species which have been hitherto included in *Aphelenchus*

and in which the males lack caudal wings, must be removed from that genus, and this applies to all the true parasitic species. Steiner, in the same note, proposes the new generic name *Pathoaphelenchus* (which had previously been used by Cobb as a subgeneric name) for "*Aphelenchus parietinus*, *A. fragariæ*, *A. olesistus*, *A. ritzema-bosi*, etc," and he fully discusses the situation in a second paper (1931B).

The position, then, is that all the truly parasitic species of *Aphelenchus* become species of *Pathoaphelenchus* and the semiparasitic species *avenæ* remains in the genus *Aphelenchus*. Incidentally, Steiner points out that Cobb's genus *Isonchus* now falls into the synonymy of *Aphelenchus*. The genus *Isonchus* contained a (free-living) species *radicicolus* which now becomes *Aphelenchus radicicolus:* this should not be confused with the parasitic species *radicicola* to be mentioned below.

TYLENCHUS.

In 1926 it was pointed out by Baylis & Daubney that the generic name *Anguillulina* Gervais & van Beneden, 1859, should have precedence over the name *Tylenchus* Bastian, 1865. The older name has already been adopted by some authors, and this Bureau will fall into line in future publications; all species of *Tylenchus* will henceforth be referred to as species of *Anguillulina*.

Unfortunately a further readjustment is necessitated in the case of the old species *Tylenchus hordei*. Goodey (1932) has shown that a description exactly corresponding to this parasite was given by Greeff in 1872 to a worm found in galls on the roots of grasses and named by Greeff *Anguillula radicicola* (the name *Anguillula* should not be confused with *Anguillulina*). This specific name has priority over *Tylenchus hordei* Schøyen, 1885, which therefore becomes, in accordance with the preceding paragraph, *Anguillulina radicicola* (Greeff, 1872) Goodey, 1932.

HETERODERA.

It is a relief to be able to state that the generic name *Heterodera* is in no immediate danger of being suppressed, at least in so far as concerns the species *Heterodera schachtii* Schmidt, 1871 and *H. punctata* Thorne, 1928. But unhappily the specific name *radicicola*, shown above to be the correct name for the old *Tylenchus hordei*, is the identical name which is known

everywhere in the form *Heterodera radicicola* (Greeff, 1872) Müller, 1884. By a very tangled confusion (see Goodey, 1932) Greeff's specific name *radicicola*, first applied to a description of a species of *Anguillulina*, was also applied to a species of *Heterodera*, and this cannot (under the Rules) be allowed to stand. Goodey has therefore resuscitated the specific name *marioni*, which has priority over all other synonyms, and the name of the root-knot nematode becomes *Heterodera marioni* (Cornu, 1879), Goodey, 1932.

The new names involved in these changes, so far as parasitic eelworms are concerned, may now be summarized as follows:

(1) *Pathoaphelenchus* Cobb, 1927. New genus for all parasitic species of *Aphelenchus*, which name is retained for *A. avenæ* and for the species of *Isonchus*.

(2*a*) *Anguillulina* Gervais & van Beneden, 1859. Correct genus for all species of *Tylenchus*, which name falls into synonymy.

(2*b*) *Anguillulina radicicola* (Greeff, 1872) Goodey, 1932. Correct name for *Tylenchus hordei*, the name *hordei* now falling into synonymy.

(3) *Heterodera marioni* (Cornu, 1879) Goodey, 1932. Correct name for *Heterodera radicicola*, the name *radicicola* having been transferred to *Anguillulina*.

HOSTS OF *HETERODERA MARIONI*.

Before proceeding to the question of identification it will be desirable to refer to the early records of the root-knot eelworm and its hosts. It has been pointed out that Greeff described an *Anguillulina* species from grasses and called it *radicicola*, and that this name afterwards became attached to the root-knot eelworm. The result has been that subsequent authors have included these grasses as hosts of the latter, whereas they were actually discovered to be hosts of the old *Tylenchus hordei*. The Bureau has, not unnaturally, followed the authorities in including these grasses in the host-list contained in the monograph "The Root-infesting Eelworms of the Genus Heterodera" (1931, see pp. 20 & 21 under *Gramineæ* and footnote to host No. R 209). The

following species of grasses should therefore be deleted from the list (*fide* Goodey, 1932, p. 27) :

R 201.—Agropyron repens.
R 209.—Elymus arenarius.
R 213.—Poa annua.
R 214.—Poa pratensis.

Identification.

Those who have had some experience in the identification of plant-parasitic eelworms will realize that it is quite impossible to prepare a short key covering all the species of these parasites. Their identification requires trained experience and a knowledge of minute anatomy which could not be conveyed in any publication short of a text-book. It has been found possible, however, to provide a key to the four genera of true plant parasites : *Pathoaphelenchus*, *Anguillulina*, *Heterodera* and *Tylenchulus*. Unfortunately the position is greatly complicated by the existence of numerous species of semi-parasitic and saprophytic eelworms belonging to genera widely different from the four mentioned above. Many of these live normally around the roots or between the leaf sheathes of plants, and as a result of a too hasty examination of material it is quite possible to be misled into supposing that some of these are true parasites from the inner plant tissues. Furthermore, where lesions occur, some eelworms which are not in themselves true parasites may enter the tissues ; and if for any reason rotting of some portion of the plant has set in, then there may be expected a whole fauna of saprophytic eelworms which have entered from the outside to feed upon the products of decomposition. These remarks are made not to dissuade agricultural officers from taking an interest in eelworm diseases but rather to advise them of some of the pitfalls, and incidentally to discourage the too hasty creation of " new species " of plant parasites.

Differential diagnosis.

The members of the three chief parasitic genera are all very closely similar in structure : in all three, for instance, the alimentary tract shows the following features :

1. An anterior mouth leading into a narrow tubular buccal cavity in which lies a stylet or spear.

2. An œsophagus having a median rounded or ellipsoidal muscular bulb and a posterior glandular region.

3. An intestine extending practically throughout the rest of the body and connected to the anus by a short, narrow rectum.

Some of the more important differential features may be summarized under the following heads:

1. General Body Form.

Pathoaphelenchus and
Anguillulina: Adults of both sexes worm-like.
Heterodera: Adult females swollen and sac-like, males worm-like.

2. Female Characters.

Pathoaphelenchus: Vulva post-equatorial in position; gonad single and anterior, a post-vulval uterine sac frequently (but not always) present.

Anguillulina: Vulva equatorial or post-equatorial: in the former case gonads paired and outstretched anteriorly and posteriorly respectively; in the latter case gonad single and outstretched anteriorly with a post-vulval uterine sac usually present.

Heterodera: Vulva terminal or sub-terminal, gonads paired.

3. Male Characters.

Pathoaphelenchus: Tail usually tapering, lateral caudal wings absent; spicules paired, thorn-shaped, laterally flattened and very closely applied to each other; gubernaculum absent; caudal papillæ present.

Anguillulina: Tail usually tapering, lateral caudal wings present and often prominent; spicules paired, rather divergent anteriorly; gubernaculum present; caudal papillæ absent in some species.

Heterodera: Tail bluntly rounded, lateral caudal wings absent but cuticle somewhat flanged laterally; spicules paired and divergent anteriorly, gubernaculum present; caudal papillæ present but minute and very difficult to locate.

4. Œsophageal Glands.

Pathoaphelenchus : Posterior region of œsophagus made up of three uninucleate gland-cells lying in a row dorsal to the beginning of the intestine. The opening of the dorsal cell lies within the muscular bulb about halfway between the front edge of the bulb and the central crescentic thickenings of the lining. Openings of the two other gland-cells just behind these crescentic thickenings.

Anguillulina : Posterior region of œsophagus made up of three uninucleate gland-cells present most frequently in the form of a pyriform or spatulate swelling, but sometimes, as in *A. pratensis*, *A. musicola* and *A. similis*, in the form of an elongated cell-group lying obliquely ventral or dorsal to the beginning of the intestine. Opening of dorsal cell by a short duct immediately behind the base of the stylet ; opening of the other two cells as in *Pathoaphelenchus*.

Heterodera : Posterior region of œsophagus made up of three uninucleate cells, best seen in larvæ or adult male, very difficult to distinguish in ripe females, lying as an oblique cell-group ventral to beginning of intestine. Openings of cells into lumen of œsophagus as in *Anguillulina*.

5. Stylet.

Pathoaphelenchus : In two parts, an anterior conical joined to a posterior cylindrical region ; base of latter simple or with three rounded knob-like thickenings.

Anguillulina : In two parts as in *Pathoaphelenchus*, base practically always with three swollen thickenings.

Heterodera : In two parts as above ; base with three large knob-like thickenings.

The characters of the genus *Tylenchulus* which contains only the one species *semipenetrans* may be indicated as follows :—

In most respects showing the characters of *Anguillulina* but differing in that (i.) there is no functional anus, (ii.) the excretory pore in or near the middle of the body, (iii.) the male is without caudal wing-like expansions of the cuticle, (iv.) the male practically loses the stylet at the first moult (v.) the posterior region of the female becomes swollen and sac-like at

maturity and the cuticle is much thickened, (vi.) the vulva lies in a deep suture and is sub-terminal in position.

It differs from Heterodera in that the gonad in the female is single and not double.

REFERENCES TO SPECIES.

Having given this brief differential diagnosis for the plant-parasitic genera, we can now proceed to mention a few of the key-descriptions of important parasitic species. In this connection it is useful to remember that, while the three species of *Heterodera* and the single species of *Tylenchulus* are all parasitic, the genera *Pathoaphelenchus* and *Anguillulina* both contain certain free-living species which, of course, will not be referred to here. In the following list the references are indicated by author and date (they are given in full at the end), and for each species the principal host or hosts are stated.

A. Species of the genus *Pathoaphelenchus* Cobb, 1927.

Synonym: *Aphelenchus* Bastian, 1865 (in part).

References: For all species see :—

Goffart, 1930.

Goodey, 1928A.

Hosts :—

P. cocophilus : Coconut palms, associated with " red-ring " disease.

P. fragariæ : Strawberries, associated with " cauliflower " and " red-plant " diseases.

P. olesistus : Ferns, etc., associated with leaf-blotch.

P. olesistus var. *longicollis :* Violets, found in galls at bases of leaf and flower stalks.

P. ribes : Blackcurrants, found in diseased buds.

P. ritzema-bosi : Chrysanthemum, associated with leaf-blotch.

P. subtenuis : Narcissus, found in diseased tissue in upper part of bulbs and associated with diseased condition of the leaves.

B. Species of the genus *Anguillulina* Gervais & van Beneden, 1859.

Synonym: *Tylenchus* Bastian, 1865.

A. agrostis.

Reference: Goodey, 1930.

Hosts: Grasses, causing flower-galls and associated with stunting of the panicle.

A. angusta.

Reference: Butler, 1913.

Host: Rice, associated with "Ufra" disease.

A. balsamophila.

Reference: Thorne, 1926.

Hosts: Balsam root, Mule ear, causing leaf-galls.

A. dipsaci.

References: Marcinowski, 1909.
Ritzema Bos, 1888-1892.

Hosts: Oats, Potatoes, Narcissus and over 100 other spp., causing galls on, and/or associated with extensive rotting of, stems (above or below ground) and leaves.

A. graminis.

Reference: Goodey, 1927.

Hosts: Grasses (*Festuca* spp.) causing leaf-galls.

A. millefolii.

Reference: Marcinowski, 1909.

Hosts: Yarrow, etc. (*Achillea* spp.), causing leaf-galls.

A. musicola.

Reference: Goodey, 1928B.

Hosts: Bananas, Vines, associated with diseased roots.

A. pratensis.

Reference: Cobb, 1917.

Hosts: Cotton, Potatoes, and over 20 other spp., associated with diseased roots.

A. radicicola.

Synonym: *Tylenchus hordei.*

Reference: Goodey, 1925.

Hosts: Barley, etc., causing root-galls.

A. similis.

Reference: Cobb, 1915.

Hosts: Sugar cane, Banana, associated with diseased roots.

A. tritici.

References: Byars, 1920.
Marcinowski, 1909.

Host: Wheat, causing flower-galls which characterize the disease "Ear-cockle."

C. Species of the genus *Heterodera* Schmidt, 1871.

Adult females in, or in the form of, galls attached to roots.

H. marioni.

Synonym: *H. radicicola.*

References: Marcinowski, 1909.
I.B.A.P., 1931.

Hosts: A range of over 500 species: see References.

H. punctata.

References: Thorne, 1928.
I.B.A.P., 1931.

Host: Wheat.

H. schachtii.

References: Marcinowski, 1909.
I.B.A.P., 1931.

Hosts: Beet, Potatoes and about 70 other species: see References.

D. Species of the genus *Tylenchulus* Cobb, 1913.

T. semipenetrans.

References: Cobb, 1913—1914.

Hosts: *Citrus* spp., attached to roots (like *Heterodera* spp.).

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Journal of Helminthology, Vol. x, *Nos.* 2-3, *June*, 1932, *pp.* 65-66.

An Experimental Infection of the Rabbit with *Capillaria hepatica* (Bancroft, 1893).

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Although several records now exist of the occurrence of *Capillaria* (*Hepaticola*) *hepatica* (Bancroft, 1893) as a natural infection of the wild rabbit the attempts which have been made to infect this host with eggs obtained from an infection in the rat have not been completely successful. Nishigori (1925) states that although this parasite can infect the rabbit and shew some development it does not reach maturity, while Saito (1925), in the English account of his paper given in *The Japan Medical World* states that " In the rabbit the larvæ might develop into maturity and cause pathological changes but do not multiply."

These results suggest that the parasite occurring naturally in the rabbit might be, at least, a different strain of *C. hepatica* from the one found in the rat. A recent experiment carried out by the present writer does not, however, confirm the findings of the Japanese workers.

Through the kindness of Professor Leiper the writer obtained a culture of embryonated eggs which had been obtained from the liver of a rat infected with *C. hepatica*. The culture which contained a very large number of eggs was fed to two young rabbits on November 27th, 1931. The rabbits at the time of the experiment were five weeks old.

Twenty-nine days after the commencement of the experiment one of the rabbits was found dead, and the other died two days later. It was found in the post-mortem examination that death was due to the extensive damage to the liver caused by the presence of a very large number of *C. hepatica*. The majority of the worms had not reached maturity, but a fair number contained fully developed eggs, and in a few instances eggs had already been laid and were found in the tissue surrounding the worms.

Unhappily it was not possible to make a detailed study of the anatomy of the worm, although several large fragments were obtained. Two of these fragments of female worms gave measurements of 22 mm. and 28 mm. respectively, while in one worm a complete portion from the head to the vulva measured 7 mm.

In a recent paper, Baylis (1931) has shewn that there is a spicule in the male and that bacillary bands are also present in *C. hepatica*. These findings were confirmed by the present writer in his observations on the worms obtained in the liver of the experimental rabbits. Ten spicules were examined, and these gave a length varying from 0·247 mm. to 0·310 mm., with an average of 0·268 mm. These measurements are appreciably less than those given by Baylis, and it was also found that the tip of the spicule does not terminate in a sharp point as described by this author.

In view of these differences, and having regard to the fact that Baylis based his observations on worms from the liver of *Apodemus sylvaticus*, the existence of more than one species within the range of hosts from which *C. hepatica* has been recorded, seems a possibility. A detailed study of these Capillarid worms of the liver is, however, a difficult matter, and the character of the eggs forms, as a rule, the only means of identifying the parasite.

An examination of some sixty eggs from the worms found in the experimental rabbits gave measurements varying from 0·051 mm. to 0·062 mm. in length, and 0·028 mm. to 0·034 mm. in width, with an average of 0·0561 mm. by 0·0325 mm.

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Journal of Helminthology, Vol. x, *Nos.* 2-3, *June,* 1932, *pp.* 67-74.

On the Experimental Development of *Bothridium (=Solenophorus) pythonis* de Blainville, 1824, in *Cyclops viridis* Jurine, 1820.

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Three species, and one variety, of the pseudophyllid genus *Bothridium* de Blainville, are known to occur in pythons. *B. ovatum* occurs in the African python (*P. sebæ*) : *B. pythonis* in the Indian python (*P. molurus*) and *B. pythonis* var *minor* in *P. reticulatus,* the Indo-Malayan python ; while Maplestone and Southwell (1923, p. 317) record another species, *B. ornatum* from the Australasian python (*P. spilotes* var *variegatus*). The literature on this genus appears, so far, to have dealt only with morphology and taxonomics. Joyeux and Baer (1927, p. 126) describe the anatomy and relationships of *B. ovatum, B. pythonis* and *B. pythonis* var. *minor*. Braun (1894-1900, p. 1690) gives a brief description, accompanied by very detailed figures, of the anatomy of *B. pythonis* and also figures the embryonated ovum (pl. lviii, fig. 8). This is the only figure of any developmental stage of the parasite which the writer has been able to discover. Southwell (1930, p. 58) records the worm from *P. reticularis* and *P. molurus,* in Bengal, Nepal and Ceylon, and summarises its anatomy. He also mentions its occurrence in a tiger which he thinks had been eating a python. No account of the life-cycle of any species of *Bothridium* appears to have been written. When, therefore, in February, 1932, some living *Bothridium* arrived in the Helminthology Department, it was resolved to discover how far its development resembled that of other better-known Psuedophyllids.

The work was carried out in the London School of Hygiene and Tropical Medicine, under the supervision of Professor R. T. Leiper F.R.S., to whom I am greatly indebted for the material and for advice and assistance.

The material consisted of a heavy intestinal infection of an Indian python (*P. molurus*) with *B. pythonis*. The python died in the London Zoological Gardens, after a life there of only 24 days. The worms were sent alive, firmly attached to the intestinal mucosa by their tubular bothridia. On being left in cold tap water overnight the worms loosened their hold and gravid segments were collected and kept in an ice chest, at a temperature of 5-7° C, at which temperature the ova will remain viable for at least a month. Ova were teased out of the uturus and cultured in tap water (which had been boiled to sterilise against *Catenaria*, etc.) at various temperatures.

The Ovum. (Fig. 1.)

The *Bothridium* egg is typical of the Pseudophyllidea : i.e., thin-shelled, operculate and compound. Ova teased out of the uterus are normally packed with spherical, granular, yolk cells surrounding the embryo. As the embryo develops the yolk cells degenerate, leaving some granular, residual protoplasm. A few ova, teased out from gravid segments, showed the onchosphere already fully formed, but usually this stage develops only after extrusion. A typical egg measures $60\mu \times 45\mu$ and its operculum, which is saucer-shaped, 16μ in diameter. The onchosphere, *in ovo*, measures about $40\mu \times 30\mu$, but is variable in shape. It is surrounded by a thin chitinised membrane, the forerunner of the embryophore. Braun's figure is fairly representative, but omits the operculum.

The Coracidium. (Fig. 2.)

Once expressed from the uterus the ova develop rapidly at favourable temperatures. Egg cultures set out at (1) laboratory temperature (14-19° C) ; (2) 22·3°—23·2° C, and (3) 29·0°—29·5° C, produced coracidia on the 3rd, 2nd and 1st subsequent day, respectively. Although experimental results were not very uniform, it is obvious that a temperature in the neighbourhood of 29·0° C is extremely favourable to development. This is what one would expect when dealing with a tropical parasite. The higher the temperature the sooner the coracidia appear.

The coracidia appear in periodical " waves." A typical coracidium measured just before death had a diameter (including the cilia) of $51\mu \times 45\mu$. The onchosphere measured $39\mu \times 42\mu$. The maximum diameter taken for a coracidium was 60μ. Both the coracidium as a whole, and

the onchosphere within it, are very plastic in their shape, which is sometimes spherical, sometimes elongate. Nuclei can be distinguished in the onchosphere, but the delineation of the cells is very indistinct. The nuclei are less distinct in the embryophore which appears as a granular, ciliated membrane, chitinised externally. The six embryonic hooks measure 9—12μ long and move independently. There is a single pair of flame cells. Rosen (1918-1919) has described and figured the coracidia of several Pseudophyllids from which the embryos of *Bothridium* may be distinguished by the following characteristics.

In *Diphyllobothrium latum* the ratio of the length of the hooks to the diameter of the onchosphere is 1 : 2. In *B. pythonis* it is 1 : 4 (approximately). A closer resemblance is to the coracidium of *D. mansoni*, as figured by Brumpt (1927, p. 599). Here, however, the hooks are yet smaller, in relation to total diameter, than in *Bothridium*. The embryo of *Tricenophorus* (Rosen 1, p. 31) does not show the rotatory movements of *Bothridium*, is larger (up to 65μ) and has narrower, slenderer hooks, and the onchosphere frequently occupies only a small part of the space enclosed by the embryophore. *Abothrium* has a non-ciliated embryo. (Rosen, 1918, p. 38.) That of *Ligula* (Rosen, 1929, p. 6) has a much thicker embryophore and moves more slowly.

The coracidia of *B. pythonis* are pelagic in habit, rising at least several cm. above the bottom and cruising along, steadily and rapidly, with a lateral rotatory movement, mentioned above, and also seen in *D. latum*. While in motion these embryos show a constant polarity, the hooks being always posterior, this pole representing the " tail " of the future procercoid. The variability of outline, already noted, is also seen in *Abothrium*. Our observations show that the coracidium of *B. pythonis* has very close affinities with that of *D. mansoni*.

Infection of the First Intermediate Host.

Cyclops viridis Jurine, 1920 was found to be highly susceptible to infection with the onchospheres, and is possibly the optimum *Cyclops* for this worm. *C. viridis* is a littoral species with a wide palæarctic and nearctic range, easily cultured in tap water at laboratory temperature. The males are creamy white, the females are larger and darker. The diagnostic characters of the species are: (1) the rudimentary fifth foot,

which is composed of two segments and carries two long setae and one short one ; (2) the first antennæ which are composed of 17 segments of which the third (from the base) is short and annular ; the seventh is relatively long, as are also the last three ; and the eighth, ninth and eleventh segments each bear a conspicuously long seta. (See Ward & Whipple, p. 775.)

A few *Cyclops* were isolated in a watch glass, containing a rich culture of coracidia and kept at 29·0° C—29·5° C. The result was such a heavy hyper-infection of the *Cyclops* that sickness, immobility and even death resulted. As many as 30 onchospheres were seen in one *Cyclops* under these conditions. In the case of reasonable infections, however, the *Cyclops* shows no obvious ill effects. As many as 15 developed procercoids were seen in a single *Cyclops* which still retained its activity. There is, therefore, no reason to regard a normal infection as being pathogenic to the host. The males are notably more susceptible to infection than the females, but both sexes are infected. So far as can be determined from personal observation, the mechanism of infection would appear to be as follows: The coracidia, on being swallowed by the copepod, lose their embryophores. The onchosphere is then passed backwards into the abdominal part of the gut, by peristalsis of the gut-wall, and there, breaking out into the abdominal cavity, wanders forward into the cephalo-thoracic cavity, where development proceeds. This hypothetical view is based upon the distribution of various stages within a *Cyclops*. Fig. 8 depicts an infected *Cyclops* and Fig. 8a is a freehand drawing of the fifth foot of *C. viridis*.

Development of the Procercoid.

Within the cephalo-thoracic cavity of the *Cyclops*, the onchosphere, whose embryophore is now replaced by a definite cuticle, commences to elongate. The rate of development varies considerably with individual onchospheres even within the same *Cyclops*. After passing through an elliptical stage (fig. 3), the parasites show definite signs of elongation about 6 days after infection. Fig. 3 shows an onchosphere squeezed out of a recently infected *Cyclops*. The thin spherical membrane attached to it is considered by the writer to be a cast cuticle. If this surmise is correct, it would appear that, in the course of development, the procercoid undergoes not less than 2, and probably more ecdyses. Figs. 4 and 5 show

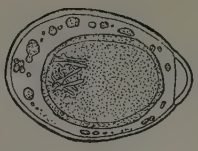

Fig. 1

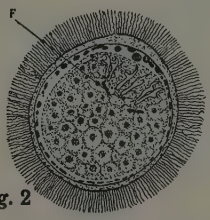

Fig. 2

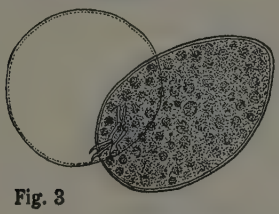

Fig. 3

Fig. 7

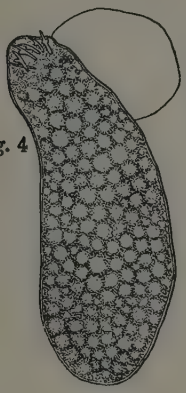

Fig. 4

Fig. 5

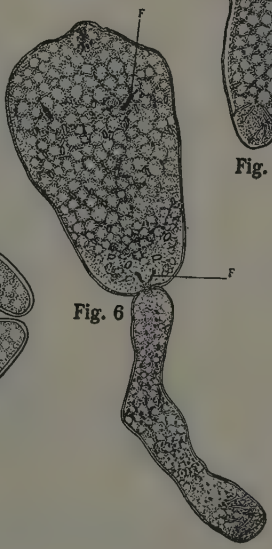

Fig. 6

Fig. 1 ·06 mm

Figs. 2 3 7 ·05 mm

Figs. 4 5 6 ·1 mm

Fig. 1. Embryonated ovum.

Fig. 2. Coracidium.

Figs. 3-7. Developmental stages of procercoid.

F = flame cells.

developing procercoids teased out of a *Cyclops* infected 14 days previously. Fig. 4 shows the first suggestion of a caudal constriction and an old cuticle. Fig. 6 shows a much more advanced constriction and a well-marked cuticle nearly ready to be cast. The caudal constriction appears to require about 14 days to develop. After 17-18 days' development within the *Cyclops*, the procercoid presents the appearance shown in fig. 6. Its shape is now reminiscent of a cercaria, and the caudal constriction is nearly complete. Constant contraction and expansion of both halves make it hard to give an accurate linear measurement ; but 260μ long seems to be fairly average for this stage. This is smaller than most known procercoids. The cephalic half now shows two pairs of flame cells, one pair quite near the constriction, the other further forward ; and solid dark bodies, presumably chalky concretions, are seen developing in both halves. The anterior part of the cephalic half shows minute cuticular bristles. Between the 18th and 20th day the constriction breaks down and the " tail " is lost, leaving a mature, tail-less procercoid (fig. 7). This stage shows the rudiments of four excretory canals converging at the anterior extremity and a characteristic caudal induration of the cuticle. The cellular structure is now very indistinct, the whole appearance becoming more hyaline and less dense than in previous stages. The mature procercoids float freely in the cephalo-thoracic cavity of the cyclops and preserve their contractibility throughout development. The number developing in one cyclops varies from 1-15. They reach maturity in about 3 weeks.

Affinities.

The procercoid shows certain morphological criteria by which it can be distinguished from those of other Pseudophyllids described in Rosen's papers. The outstanding characteristics of the procercoid stage of *B. pythonis* are :—

(1) The absence of cephalic grooves.

(2) The relatively long caudal region : often nearly as long as the body of procercoid.

(3) The comparatively small size and the large number present in a single *Cyclops*.

(1) Serves to distinguish the procercoid of *B. pythonis* from those of

Ligula, *Diphyllobothrium* and *Triænophorus*. *Ligula* has also a characteristic mucilaginous investment, here lacking, and a shorter tail. An unpublished drawing of the procercoid of *D. mansoni*, by Macdonald, shows six pairs of flame cells and three pairs of excretory canals as against

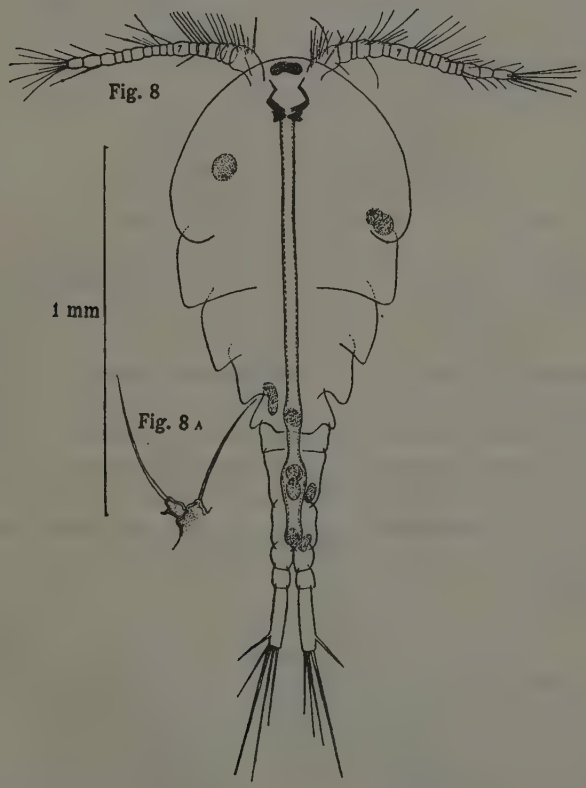

Fig. 8. A recently infected *Cyclops* showing 10 onchospheres.
Fig. 8A. Fifth foot of *Cyclops viridis*: an important diagnostic character.

two pairs of flame cells and two pairs of excretory vessels observed in *B. pythonis*. The procercoid of *Triænophorus* has a moderately elongated "tail" but it is shorter than in *Bothridium*. *Triænophorus* does, however,

show the cuticular induration at the posterior end of the cephalic half which is a characteristic of the species under discussion. The closest resemblance is to the procercoid of *Abothrium infundibuliformis* (Rosen, 1918), a parasite of the pyloric cæca of the lake trout (*Trutta lacustris*) which has a long attenuated caudal region closely resembling that of *Bothridium*, two pairs of excretory canals and no cephalic grooves. On the other hand, *Abothrium* shows no posterior invagination of the cephalic half and no cuticular bristles. In any case, the non-ciliated, inactive embryo of *Abothrium* is distinctive.

Note on Technique Employed.

The writer is deeply indebted to Mr. W. A. Macdonald of the Helminthology Department for invaluable help in this direction.

Cyclops were normally examined for infection under a 2/3 inch objective in a hanging drop of water. For detailed study of the procercoids, the latter were teased out of the *Cyclops* and examined in physiological saline with the 1/6th inch and oil-immersion objectives. Coracidia are best mounted in a small drop of water under a coverslip, ringed with vaseline, and studied as their metabolism commences to slow down. Fairly satisfactory permanent preparations of infected *Cyclops* were obtained by fixing the latter, for a few minutes, in warm Bouin's picro-formol reagent ; washing in several changes of 70 per cent. spirit to remove the picric acid ; transferring to glycerine-alcohol and leaving overnight, exposed to the air, to evaporate the alcohol, and finally mounting in glycerine-jelly.

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Journal of Helminthology, Vol. x, *Nos.* 2-3, *June,* 1932, *pp.* 75-180.

The Genus *Anguillulina* Gerv. & v. Ben., 1859, vel *Tylenchus* Bastian, 1865.

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Introduction.

The purpose of the present paper is to bring together brief descriptions of the various species of the genus *Anguillulina*, more generally known under the synonymous generic name of *Tylenchus* Bastian, 1865. In the case of the plant-parasitic species, in addition to particulars on dimensions and morphology, data are given on life-history, hosts and geographical distribution ; such matters as symptoms, pathology and methods of control are not dealt with.

The plant-parasitic species are considered first, starting with the type species, *Anguillulina tritici*, which gives rise to galls in ears of wheat. Then follow other species causing galls on aerial parts of plants and from these we pass to parasites, such as *A. dipsaci*, giving rise to more generalised symptoms of disease. The species attacking aerial parts of plants, or shoot structures, having been dealt with, those parasitic on roots are next considered, and then the free-living species. Species inquirendæ and nomina nuda next come under review, then those species which are brought into and removed from the genus in the present paper are noted and an alphabetical list of *Tylenchus* species is given with particulars as to the present status of each species.

In the body of the paper all the species are dealt with in the same order as far as possible. First the name and synonyms are given ; then

follow dimensions and a brief description of the anatomy of the adults. Female and male characters are next considered and particulars about eggs and larvæ are given where information as to these is available. In the case of plant-parasitic species, a brief account of the life-history is given as well as a list of hosts and countries from which the species has been recorded. In the case of free-living species, occurrence and relationships are briefly dealt with. After each species numbers are given which refer to the list of references at the end of the paper. This includes important papers bearing on questions of biology and life-history as well as on purely morphological matters.

A word or two are perhaps called for concerning the decision to use the generic name *Anguillulina* in preference to *Tylenchus*. The latter certainly has the sanction of long usage and wide acceptance in scientific publications but must, unfortunately, give place to *Anguillulina* which antedates it. It may be claimed by some that the use of the name *Anguillulina* is likely to lead to confusion with the generic name *Anguillula* and its derivatives such as the sub-family name *Anguillulinæ*. This may be so, but on this point the writer would venture to repeat an opinion which he put forward in 1929, namely that since Peters has shown that there are very good reasons for dropping the name *Anguillula* entirely and has proposed in its place the name *Turbatrix*, this confusion need not arise if workers will but make use of this generic name instead of *Anguillula* when writing of the vinegar eelworm, etc.

As dealt with in the following pages, the genus *Anguillulina* is not considered to be so wide and comprehensive as it is by Baylis and Daubney (1926) who included the following genera as synonymous with it :— *Anguina* Scopoli, 1777 ; *Tylelenchus* Bastian, 1865 ; *Tylenchus* Bastian, 1865 ; *Eutylenchus* Cobb, 1913 ; *Atylenchus* Cobb, 1913 ; *Tylenchorhynchus* Cobb, 1913 ; *Dolichodorus* Cobb, 1914 ; *Iotonchium* Cobb, 1920 ; *Aphelenchulus* Cobb, 1920 ; *Parasitylenchus* Micoletzky, 1921 ; *Paratylenchus* Micoletzky, 1921 ; and *Chitinotylenchus* Micoletzky, 1921. The writer includes only the following as synonyms of it :—*Tylelenchus* Bastian, 1865 ; *Tylenchus* Bastian, 1865 ; and *Chitinotylenchus* Micoletzky, 1921.

Another point of systematic interest which may be noted here is that the writer has not followed Micoletzky (1921) in removing *Tylenchus robustus* de Man, *T. multicinctus* Cobb and *T. olaæ* Cobb to the genus

Tylenchorhynchus Cobb, 1913 but has retained them in *Anguillulina*. It is in fact a little difficult to understand why Micoletzky adopted this course since Cobb states in his generic description of *Tylenchorhynchus* that the mouth stylet is " minute " whereas in the three species of *Tylenchus* mentioned above it is of great size and is very stoutly built.

ACKNOWLEDGMENTS. The writer desires to acknowledge gratefully the facilities generously placed at his disposal by Prof. R. T. Leiper for the use of papers from his private library of helminthological literature and to thank the Imperial Bureau of Agricultural Parasitology for their good offices in securing the loan of the paper by Bally and Reydon on nematodes from coffee roots.

Family : *ANGUILLULINIDÆ* Baylis and Daubney, 1926.
Sub-family : Anguillulininæ Baylis and Daubney, 1926.
Genus : Anguillulina Gervais and van Beneden, 1859.

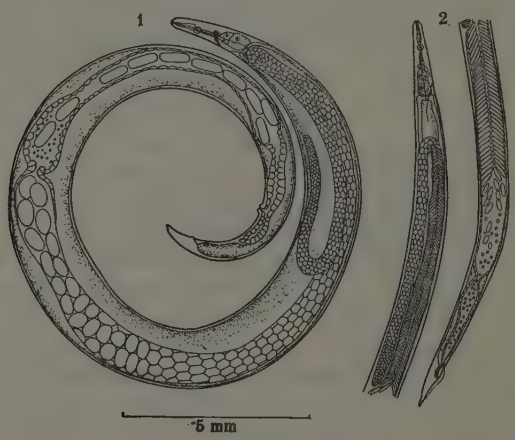
DIAGNOSIS. Adults of both sexes worm-like ; cuticle with transverse striations. Head without distinct lips but formed by the amalgamation of six lips and often showing outlines of these as six radial ridges on surface of head ; latter without setæ or bristles. Stylet in form of slender tube made up of two parts ; an anterior conical and a posterior cylindrical part, latter usually with three basal, knob-like thickenings. Lateral organs or amphids as fusiform bodies, one on either side of stylet in true lateral position. Œsophagus with median muscular bulb with more or less distinct crescentic thickenings of lumen at its centre and a posterior glandular region containing three uni-nucleate œsophageal (salivary) gland-cells. Openings of latter into lumen of œsophagus as follows :—Dorsal one by short duct just behind base of stylet, two sub-median cells opening within muscular bulb just behind crescentic thickenings of lumen. Vulva either equatorial or post-equatorial in position. Ovary single or paired ; in former case vulva generally well behind middle of body, ovary outstretched anteriorly and a post-vulval uterine sac present. When the ovaries are paired the vulva is near middle of body and ovaries are opposed and outstretched before and behind. Spicules paired and divergent ; a gubernaculum present as a rule. Tail with caudal alæ, sometimes forming a bursa enclosing tip of tail. A post-anal caudal papilla sometimes present on either side.

PLANT-PARASITIC SPECIES ATTACKING SHOOT STRUCTURES.

ANGUILLULINA TRITICI (Steinbuch, 1799) Gerv. and v. Ben., 1859.

Syn. *Vibrio tritici* Steinbuch, 1799.
Vibrio tritici Bauer, 1823.
Rhabditis tritici Dujardin, 1845.
Anguillula graminearum Diesing, 1851, in part.
Anguillula scandens Schneider, 1866.
Tylenchus tritici Bastian, 1865.

MORPHOLOGY. Dimensions :—*Female :* length, 3 mm. to 5 mm. ; breadth, 0·1 mm. to 0·2 mm. ; œsophagus, 0·15 mm. to 0·2 mm. ; tail, 0·09 mm. to 0·1 mm. ; stylet, 0·01 mm. $a = 30–25$, $\beta = 25–20$, $\gamma = 50–32$, V = 90%–94%.



Anguillulina tritici.

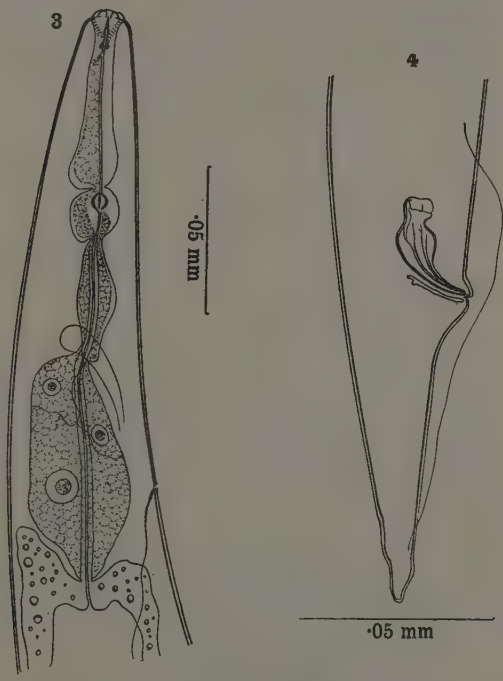
Figs. 1 and 2. Adult female and male under low magnification, lateral view.

Male : length, 2 mm. to 2·5 mm. ; breadth, 0·07 mm. to 0·1 mm. ; œsophagus, 0·15 mm. to 0·2 mm. ; tail, 0·08 mm. to 0·1 mm. ; spicules, 0·035 mm. ; gubernaculum, 0·018 mm. $a = 29–25$, $\beta = 13–12$, $\gamma = 28–25$.

Adults are found in developing galls whilst these are still soft and

green within the ear before it emerges from the ensheathing leaves. They are easily visible to the naked eye.

Cuticle transversely striated. Body tapering anteriorly and posteriorly, tail conical with a peg-like tip. Head narrower than body and offset by constriction, shaped like a flattened disc and showing six equidistant radial surface ridges. An end view of the head as figured by Steiner (1925) shows six minute papillæ, two sub-dorsal, two sub-ventral and



Anguillulina tritici

Fig. 3. Œsophageal region of adult worm highly magnified, lateral view.
Fig. 4. Male tail, lateral view, highly magnified. Transverse striæ not shown.

two lateral, the last being associated with the openings of the cephalic glands or amphids. The latter are fusiform in shape and lie on either side of the stylet. This is rather small and in two parts, an anterior steeply conical half and a cylindrical posterior half with three

distinct, rounded basal swellings. Œsophagus of variable length due to the forward growth of the ovary or testis, consisting of an anterior part about 0·01 mm. long terminating in the swollen muscular bulb, the lining of which has three crescentic thickenings ; a neck region about as long as the pre-bulbar part, and more or less twisted into an S ; the final swollen glandular region more or less pyriform in shape and containing three uni-nucleate œsophageal gland cells. The largest of these occupies the bulk of the structure and has a large nucleus, the other two cells are found towards the fore part of the posterior swelling and have small nuclei. Opening of dorsal gland cell into lumen of œsophagus by short duct on dorsal side just behind base of stylet, openings of other two cells immediately behind crescentic thickenings within muscular bulb. Nerve ring crossing neck region. Excretory pore on ventral side in vicinity of posterior swelling of œsophagus. Intestine greatly distended, connected by a short rectum to anus.

FEMALE. Nearly always coiled watch-spring wise when dissected out from galls. Vulva far back on ventral surface with prominent rounded lips. Vagina very short leading to uterus anteriorly and post-vulval uterine sac posteriorly. Walls of uterus cellular and very elastic, capable of accommodating a large number of eggs at a time. Front end of uterus swelling out to form receptaculum seminis. Latter separated from oviduct by sphincter having lips jutting into it. Oviduct continued forwards and blending with ovary ; latter gradually narrowing, usually folded once or twice on itself and terminating often in vicinity of œsophagus.

MALE. Testis anterior, commencing in œsophageal region and as in female folded once or twice on itself. Vas deferens well developed with a constriction about 0·2 mm. in front of anus. Caudal alæ arising a little in front of level of heads of spicules, widest opposite anus and uniting with body again just short of tip of tail. Spicules paired, tips pointed, broad in middle and having two ventral ridges running from point to widest part ; head with dorsal side folded over ventrally. Gubernaculum, when viewed laterally, simple but actually rather triangular in shape with the base underlying the points of the spicules.

EGGS. Average size, 0·085 mm. long by 0·038 mm. wide, may be as much as 0·13 mm. to 0·14 mm. long by 0·033 mm. to 0·063 mm. wide.

LARVÆ. First stage, 0·5 mm. to 0·6 mm. long by about 0·01 mm. wide, very delicate in appearance but showing stylet, œsophagus and intestine distinctly ; not resistant to desiccation. Second stage, 0·8 mm. to 0·95 mm. long by 0·015 mm. to 0·02 mm. wide. Structure as in first stage but more distinct, anus visible and tail with a sharp terminal process. Very resistant to desiccation, can survive in dried galls for 10 years.

LIFE-HISTORY. Second stage larva from galls invade seedlings of wheat or other host and make their way to the region of the growing point where they remain as ectoparasites. They may kill the plant or cause it to exhibit characteristic twistings and distortions of leaves and stem. Larvæ carried up by elongation of stem, change to adults within the tissues of the inflorescence. Six or more males and females to each gall in which thousands of eggs are laid. These hatch and give rise to first stage larvæ, latter rapidly grow, undergo one ecdysis and become second stage larvæ.

HOSTS. *Triticum vulgare* (wheat) very susceptible, *Secale cereale* (rye) very susceptible, *Triticum dicoccum* (emmer) very susceptible, *Triticum spelta* (spelt) susceptible, *Hordeum vulgare* (barley) practically non-susceptible.

GEOGRAPHICAL DISTRIBUTION. Europe, China, Turkestan, India, North and South America, Australia, Egypt.

REFERENCES. 11, 23, 30, 32, 34, 71, 82, 99, 100, 103, 108.

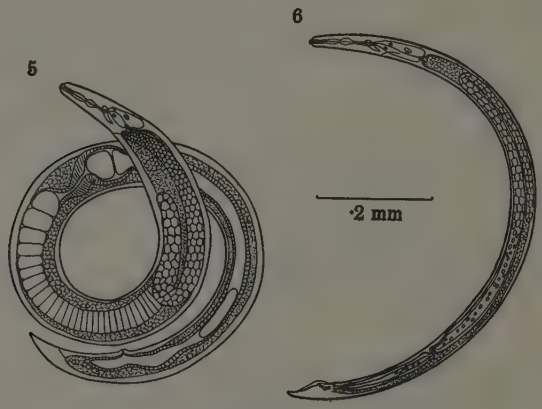
ANGUILLULINA AGROSTIS (Steinbuch, 1799) Goodey, 1932.

Syn. *Vibrio agrostis* Steinbuch, 1799.
Vibrio phalaridis Steinbuch, 1799.
Anguillula graminearum Diesing, 1851 in part.
Tylenchus agrostidis Bastian, 1865.
Tylenchus phlei Horn, 1888.

MORPHOLOGY. Dimensions :—*Female* : length, 1·5 mm. to 2·7 mm. ; breadth, 0·09 mm. to 0·14 mm. ; œsophagus, 0·18 mm. to 0·23 mm. ; tail, 0·06 mm. to 0·07 mm. ; stylet, 0·008 mm. to 0·009 mm. ; $a = 21–17$, $\beta = 11–8$, $\gamma = 44–32$, V = 87%–88%. *Male* : length, 1·1 mm. to 1·68 mm. ; breadth, 0·04 mm. to 0·06 mm. ; œsophagus, 0·15 mm. to 0·23 mm. ; tail, 0·06 mm. to 0·07 mm. ; spicules, 0·035 mm.

to 0·04 mm.; gubernaculum, 0·014 mm.; $a = 28–23$; $\beta = 9–6$; $\gamma = 23–20$.

Adults of both sexes very closely resemble those of *A. tritici* but are consistently smaller. Further description of the anatomy is unnecessary since that given for *A. tritici* applies equally well for the general structure. In addition to the consistently smaller size, the principal point of difference between the two species is in the shape of the spicules. These are built on the same plan in both species but in *A. agrostis* are of slenderer build throughout and are narrower at the widest part than in *A. tritici*. The handle region is also longer than in that species and the dorsal edge of the anterior end does not bend over ventrally to such an extent as in *A. tritici*.



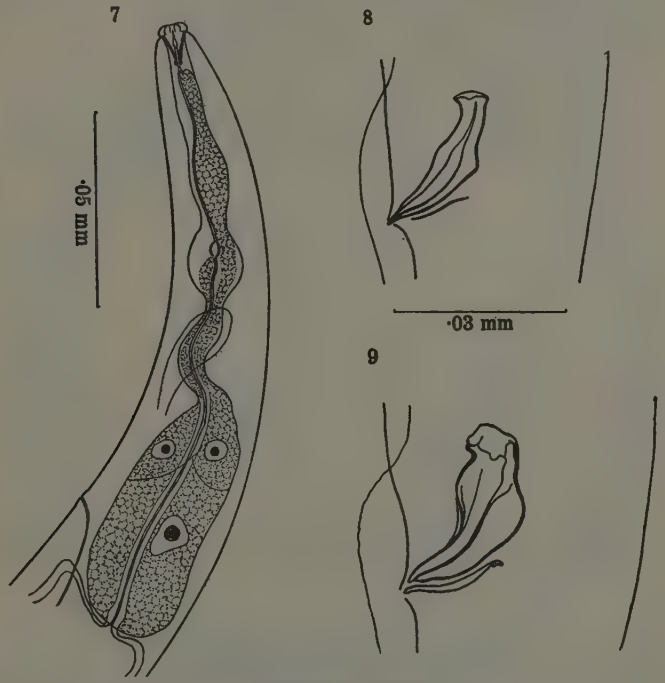
Anguillulina agrostis.

Figs. 5 and 6. Adult female and male.

EGGS. Cylindrical, with rounded ends, and showing considerable variation in size; 0·09 mm. to 0·15 mm. long by 0·03 mm. to 0·05 mm. wide.

LARVÆ. First stage larvæ, 0·55 mm. long by 0·012 mm. wide, not resistant to desiccation. Second stage larvæ, 0·75 mm. to 0·8 mm. long by 0·016 mm. to 0·018 mm. wide. Having same shape and structure as second stage larvæ of *A. tritici*. Resistant to desiccation and capable of revival after drying and re-moistening.

LIFE HISTORY. In essentials the same as that of *A. tritici*. Second stage larvæ invade grass seedlings and are carried up with the growing point. They enter the developing tissues of the inflorescence and give rise to fusiform galls in which they reach maturity. The females then lay a large number of eggs which hatch and give rise to first stage larvæ which quickly become second stage infective larvæ. The galled flowers of Agrostis and several other grasses show greatly elongated glumes and pales.



Anguillulina agrostis.

Fig. 7. Œsophageal region of adult worm highly magnified, lateral view.
Figs. 8 and 9. Spicule and gubernaculum of *A. agrostis* and *A. tritici* respectively, highly magnified, lateral view.

HOSTS. Marcinowski (1909) gives the following as showing galls due to this species:—*Agrostis alba, A. canina, A. capillaris, A. polymorpha* (*stolonifera*), *A. vulgaris, Festuca ovina, Kœleria glauca,*

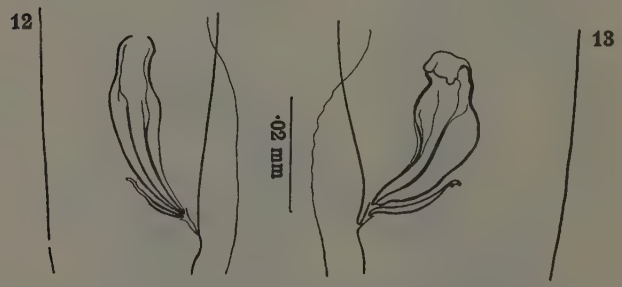
Phalaris phleoides, *Poa alpina*? and *Poa annua*. The parasite in the following is given as *A. phalaridis* (but the writer considers this a synonym of *A. agrostis*) *Phalaris phleoides*, *Phleum pratense*, *Kœleria cristata*. In addition, the following grasses are listed as having galls in the inflorescences due to unspecified nematodes: *Arundo phragmites*, *Avena elatior*, *Bromus erectus*, *Calamagrostis sp.*, *C. lapponica*, *Chætochloa sp.*, *Dactylis glomerata*, *Elymus sp.*, *Festuca duriuscula*, *F. rubra*, *Holcus lanatus*, *Poa bulbosa* var. *vivipara*, *P. pratense*.

GEOGRAPHICAL DISTRIBUTION. Europe and North America.

REFERENCES. 2, 6, 32, 39, 47, 71, 82, 108.

ANGUILLULINA GRAMINIS (Hardy, 1850) Goodey, 1932.

Syn. *Tylenchus graminis* (Hardy, 1850) Marcinowski, 1909.
Vibrio graminis Hardy, 1850.

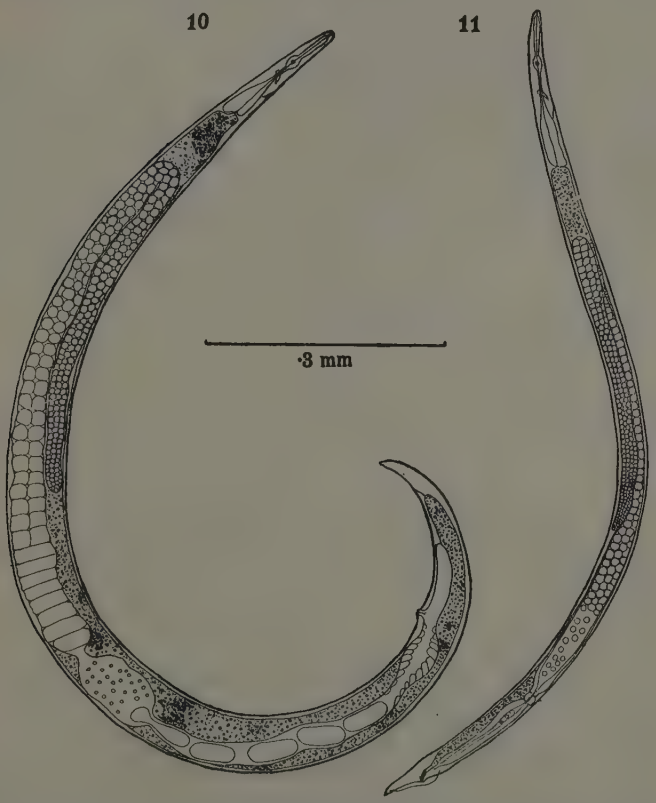


Anguillulina graminis.

Figs. 12 and 13. Spicule and gubernaculum of *A. graminis* and *A. tritici* respectively; lateral view.

MORPHOLOGY. Dimensions:—*Female*: length, 1·87 mm. to 2·7 mm.; breadth, 0·1 mm. to 0·13 mm.; œsophagus, 0·22 mm. to 0·25 mm.; tail, 0·07 mm. to 0·08 mm.; stylet, 0·01 mm.; $a = 20–18·7$, $\beta = 10–9$, $\gamma = 30–27$, V = 84%–86%. *Male*: length, 1·12 mm. to 1·58 mm.; breadth, 0·05 mm. to 0·075 mm.; œsophagus, 0·22 mm. to 0·25 mm.; tail, 0·07 mm. to 0·09 mm.; stylet, 0·01 mm.; spicules, 0·04 mm. to 0·045 mm.; gubernaculum, 0·013 mm.; $a = 22·4–21$, $\beta = 6–5$, $\gamma = 17–16$.

This species also closely resembles *A. tritici* in general shape and structure but is smaller, as the measurements show. The females do not coil up so much as do those of *A. tritici* and *A. agrostis* but are, nevertheless, usually curved towards the ventral surface. Stylet, œsophagus, intestine and gonads in both sexes have the same structure



Anguillulina graminis.

Figs. 10 and 11. Adult female and male under low magnification. Nuclei of the three œsophageal gland cells not indicated.

as in the two species already described. The spicules of the male differ from those of *A. tritici* in being slenderer and in having the anterior

end open with dorsal and ventral edges curving inwards towards each other; the dorsal side does not overlap the ventral as in *A. tritici*.

EGGS. Not measured.

LARVÆ. First stage not measured. Second stage, 0·67 mm. to 0·79 mm. long by 0·014 mm. to 0·018 mm. wide, average length, 0·728 mm. Same structure and shape as second stage larvæ of *A. tritici* and *A. agrostis*, resistant to desiccation.

LIFE HISTORY. Similar in essential to that of *A. tritici* and *A. agrostis*; the second stage larvæ invade young grass blades and give rise to purple galls measuring 1 mm. to 4 mm. long by 0·5 mm. to 2 mm. wide, within which they come to sexual maturity. Each gall usually contains two or three adults of each sex. The females lay eggs which give rise to first stage larvæ which rapidly change to second stage larvæ after one ecdysis.

HOSTS. *Festuca ovina*, *F. duriuscula*, *F. dumetorum* and *F. rubra*.

GEOGRAPHICAL DISTRIBUTION. Europe.

REFERENCES. 44, 53, 82, 84.

ANGUILLULINA MILLEFOLII (Löw, 1874) Goodey, 1932.

Syn. *Tylenchus millefolii* Löw, 1874.

MORPHOLOGY. Dimensions:—*Female*: length, 2·33 mm.; breadth, 0·11 mm.; œsophagus, 0·23 mm.; tail, 0·13 mm.; stylet, 0·0089 mm. to 0·0092 mm.; $a = 20·8$, $\beta = 10$, $\gamma = 17·7$, V = 87%–88%. *Male*: length, 1·6 mm.; breadth, 0·061 mm.; œsophagus, 0·19 mm.; tail 0·09 mm.; spicules, 0·036 mm.; gubernaculum, 0·014 mm.; $a = 26·18$, $\beta = 8·4$, $\gamma = 17·7$.

In anatomy and structure both sexes are closely similar to the adults of the three species already described.

FEMALE. In comparing Marcinowski's figure of the female with that of *A. tritici* the principal difference to be noted is that the uterus is shorter in *A. millefolii* and that the receptaculum seminis is rather elongated. The post-vulval uterine sac appears to be rather short and the anterior loops of the ovary do not reach so far forwards as in *A. tritici* though this may be due to the immaturity of the specimen figured.

MALE. The spicules, as figured by Marcinowski, are rather schematised

and it is, therefore, impossible to compare them closely with those of the three species already dealt with. They appear to have the same general shape whilst it may be noted that the caudal alæ do not surround the tip of the tail.

EGGS. No measurements given.

LARVÆ. The first stage larva is rather short and stout, having a length of 0·36 mm. with $a = 21$, whereas in the case of the first stage larva of *A. tritici*, $a = 44$. Another point of difference is that whereas the tip of the tail in larvæ of *A. tritici* is sharply pointed it is rather bluntly rounded in *A. millefolii*. The two other proportions are given by Marcinowski as $\beta = 3{\cdot}6$, $\gamma = 9$. It is not clear whether there is a distinction in size between first and second stage larvæ in *A. millefolii* such as occurs in those of the species already dealt with, nor whether one particular stage is resistant to desiccation.

LIFE HISTORY. Details are lacking. Adults and larvæ have been found in green galls on leaves and leaflets. Marcinowski considers that the larvæ can set up fresh galls so long as the plant is green, possibly by wandering out from older galls and travelling on the surface of the plant in dew or rain drops. It is unknown in what condition the parasite overwinters. Further knowledge on the biology of this species is much needed.

HOSTS. *Achillea millifolium* and *A. tanacetifolia*.

GEOGRAPHICAL DISTRIBUTION. Germany, Italy ?

REFERENCES. 74, 82, 88.

ANGUILLULINA BALSAMOPHILA (Thorne, 1926) Goodey, 1932.

Syn. *Tylenchus balsamophilus* Thorne, 1926.

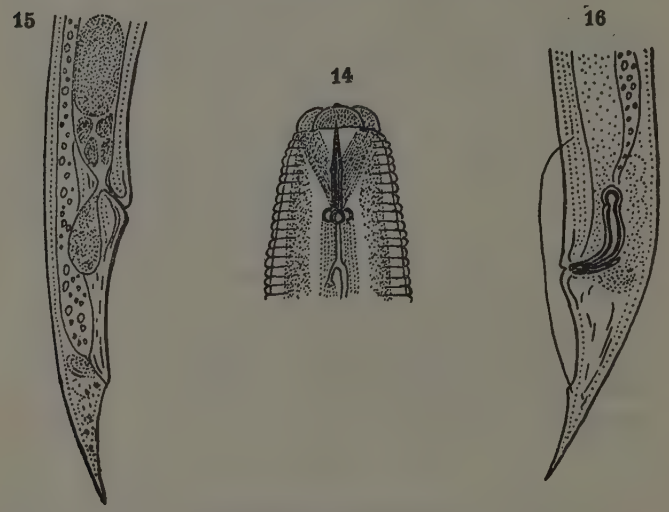
MORPHOLOGY. Dimensions :—Thorne gives the two following formulæ—

female	·7	8·	11·	W	$^{76\cdot}88\cdot^{3\cdot}$	96·6	2·6–3·4 mm.
	·7	2·5	3·1	6·	3·2	1·6	
male	·7	8·	11·	$^{81\cdot}$M	95·		1·5–2 mm.
	·7	1·8	2·2	3·4	2·		

Adults of both sexes essentially the same in structure as those of

the species already described. Cuticle transversely striated. Head in end view practically the same as that of *A. tritici*. Stylet, as measured from Thorne's fig. 2, 0·016 mm. long, which is much longer than the stylet of any of the species so far dealt with. Tail more sharply pointed than in *A. tritici*, *A. agrostis* and *A. graminis*. Post-vulval uterine sac short with rounded end.

MALE. The figure of the male tail shows the tip very sharply pointed. The caudal alæ arise with a marked convex edge well in advance of the



Anguillulina balsamophila.

Fig. 14. Head end, lateral view, × 1000.
Fig. 15. Hind end of female, lateral view, × 120.
Fig. 16. Male tail, lateral view, × 350. (All after Thorne.)

heads of the spicules, blending with the body again a little more than halfway to the tip of the tail. Spicules massive; as measured from Thorne's figure, about 0·055 mm. long with head slightly knobbed, points sharp; gubernaculum simple, about 0·018 mm. long.

EGGS. 0·06 mm. long by 0·037 mm. wide. Laid unsegmented.

LARVÆ. First stage larva 0·35 mm. to 0·4 mm. long. Growth

proceeds till pre-adult larvæ showing sexual differentiation are produced ; these have tails blunter than adults. They are quiescent and can withstand desiccation for two years. Thorne gives the following formula for them—

$$\frac{1\cdot2 \quad 11\cdot0 \quad 20\cdot \quad 91\cdot2 \quad 97\cdot1}{\cdot7 \quad 1\cdot9 \quad 2\cdot7 \quad 3\cdot \quad 2\cdot4} \quad 0\cdot9\text{–}1\cdot1 \text{ mm.}$$

LIFE HISTORY. Larvæ produced by adults within leaf galls remain active till the beginning of July but further growth ceases as galls become old and withered. Galls are carried to the ground by winter snows and in the following spring the infective, pre-adult larvæ make their way out and invade the crowns of young plants and set up galls in the leaves. Within these they rapidly become adult and in about three weeks from infection eggs are produced. There are usually from three to eight adults of each sex per gall.

HOSTS. *Balsamorhiza sagittata* (balsam root), *B. macrophylla*, and *Wyethia amplexicaulis* (mule ear).

GEOGRAPHICAL DISTRIBUTION. Utah, U.S.A.

REFERENCE. 114.

ANGUILLULINA DIPSACI (Kühn, 1858) Gerv. and v. Ben., 1859.

Syn. *Anguillula dipsaci* Kühn, 1858.
Anguillula devastatrix Kühn, 1868.
Anguillula secalis Nitschke, 1868.
Anguillula putrefaciens Kühn, 1877 or 1879.
Tylenchus dipsaci (Kühn, 1858) Bastian, 1865.
Tylenchus askenasyi Bütschli, 1873.
Tylenchus havensteinii Kühn, 1881.
Tylenchus hyacinthi Prillieux, 1881.
Tylenchus allii, Beijerinck, 1883.
Tylenchus devastatrix Ritzema Bos, 1888-92.

MORPHOLOGY. Dimensions :—*Female* : length, 0·9 mm. to 1·86 mm. ; breadth, 0·04 mm. to 0·06 mm. ; œsophagus, 0·16 mm. to 0·24 mm. ; tail, 0·08 mm to 0·14 mm. ; stylet, 0·011 mm. to 0·013 mm. ; $a = 51\text{–}31$, $\beta = 8\text{–}6$, $\gamma = 20\text{–}17$, V = 80%–82%. *Male* : length, 0·9 mm. to 1·6 mm. ; breadth, 0·03 mm. to 0·04 mm. ; œsophagus, 0·16 mm. to 0·22 mm. ;

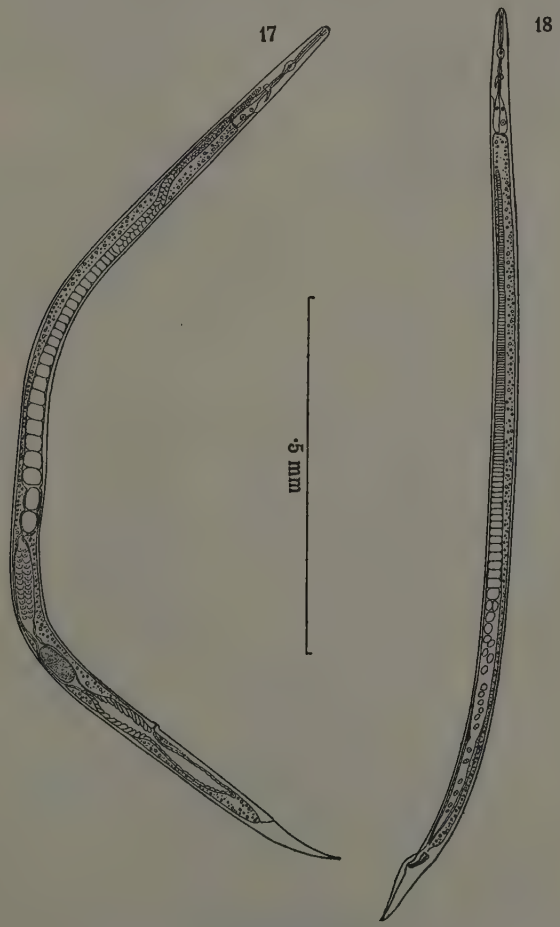
tail, 0·08 mm. to 0·1 mm.; stylet as in female; spicules, 0·025 mm. to 0·028 mm.; gubernaculum, 0·01 mm. to 0·012 mm.; $a = 55–40$, $\beta = 8–6$, $\gamma = 20–17$. The above maximum lengths do not include the very long forms recorded by Debray and Maupas, who gave lengths of 1·758 mm. to 2·216 mm. for females and 1·716 mm. to 2·016 mm. for males. Such large forms are not ordinarily met with, the average size being 1·22 mm. to 1·7 mm. for females and 1·2 mm. to 1·5 mm. for males.

Adults of both sexes are rather slender, the body tapering anteriorly in the œsophageal region and posteriorly behind the anus; tip of tail sharply pointed in both sexes. Head somewhat conical, offset from body by slight constriction; showing six radial ridges on surface. According to Steiner (1925) and Ouboter (1930) an end view of the head shows certain very small papillæ, two sub-dorsal, two sub-ventral and two lateral in position. Steiner figures them as all rather centrally placed and closely encircling the mouth aperture, the lateral pair representing the openings of the amphids. Ouboter, on the other hand, shows both the sub-dorsal and sub-ventral papillæ towards the periphery of the head and instead of figuring lateral amphidial apertures, shows something like an empty vacuole or sac in each lateral segment of the head with a papilla at the periphery. Possibly the vacuole corresponds to part of the so-called amphidial pouch.

Cuticle of body transversely striated, striæ not present on head and tip of tail. Striæ 1·28μ apart in œsophageal region to 1·92μ apart on most of rest of body. Ouboter says there are deeper-lying striæ closer together than these and having a darker appearance. Striations interrupted by lateral fields, larger striæ running as far as fields, narrower ones not reaching them. Lateral fields about 10μ wide, slightly raised above level of body, edges with small wings. Longitudinal striæ present and deeper lying.

Mouth terminal leading to narrow tubular buccal cavity about as long as depth of head. The point of the stylet lies in this tube. Stylet typical, anterior half conical, posterior half cylindrical with three rounded knobs at base. In the dorsal and ventral fields there appear to be muscles attached to the base of the stylet and inserted in the body-wall close to the head constriction.

On either side of the stylet in a lateral position is a rather fusiform amphidial pouch, broadest a little behind the base of the stylet and tapering anteriorly to a fine duct which passes through the head, posteriorly leading by a narrow duct into the substance of the body and becoming lost in the vicinity of the œsophageal bulb.



Anguillulina dipsaci.

Figs. 17 and 18. Adult female and male, lateral view.

Œsophagus typical in structure ; anterior part about one-third width of corresponding body region, bulb ellipsoidal, leading to narrow neck, very variable in length, which swells out into the terminal glandular area. This contains three uni-nucleate œsophageal gland cells sometimes arranged in file and lying more or less obliquely in body or more frequently in a somewhat pyriform group with two smaller cells towards the front and the larger cell behind. The whole mass surrounds a narrow cuticular lumen leading to intestine. Openings of glands into lumen of œsophagus typical.

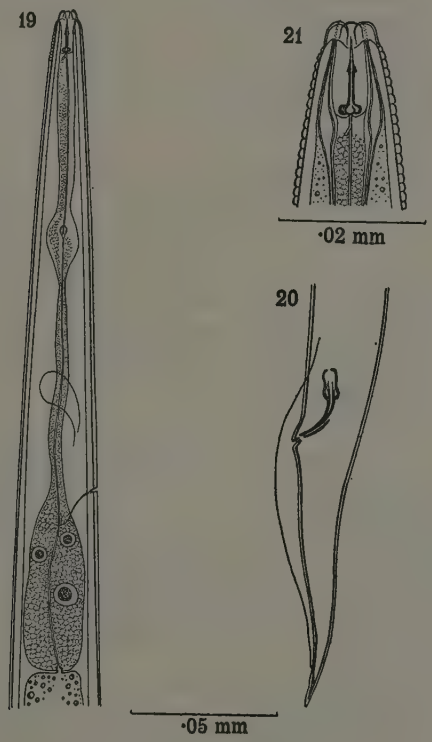
Intestine with narrow wavy cuticular lumen ; wall composed of numerous uni-nucleate cells which are, as a rule, well stocked with fatty food globules and smaller non-fatty granules. Intestine ending in rectum leading to anus. Excretory-pore ventral at about level of posterior region of œsophagus, duct leading inwards and backwards to a pyriform cell, the " renette " cell of Cobb, located on the left side of the body close to the beginning of the intestine. Connection of duct with cell very difficult to define. Nerve ring crossing neck of œsophagus.

FEMALE. Vulva in form of transverse slit with rounded lips ; vagina very short leading anteriorly to uterus and posteriorly to uterine sac, the latter often containing spermatozoa, and extending almost to level of anus. Uterus wall composed of a fairly stout epithelium of polygonal cells. At a distance in front of the vulva equal to about three times the body width, the wall of the uterus appears to be made up of three or four rows of small glandular cells. In front of this, and following another constriction, the genital tube swells into the receptaculum seminis, which again is separated by a further constriction from the ovary. The latter is made up of a long row of developing ova gradually diminishing in width and often reaching to the œsophagus. It is generally folded once or twice on itself in its anterior region.

MALE. Gonad single, anterior, often extending to œsophageal region. This testicular part has the cells arranged guinea-roll-wise. A little further back the wall thickens somewhat and spermatocytes and spermatozoa are arranged irregularly ; this region may be considered as the vesicula seminalis. The vas deferens which succeeds this has thicker walls and spermatozoa occur one by one or two at a time in it. The final narrow region has very thick walls and has been called the ductus

ejaculatorius. This and the vas deferens always lie ventral to the intestine.

Spicules paired, tips pointed, shaft gradually widening for about two-



Anguillulina dipsaci.

Fig. 19. Œsophageal region of adult, lateral view.

Fig. 20. Male tail, lateral view. Striations of cuticle omitted.

Fig. 21. Head end, highly magnified, dorsal view, showing terminal parts of cephalic glands or amphids.

thirds the total length and then expanding into a rather oblong-shaped head region the dorsal and ventral edges of which curve inwards. Two longitudinal ridges run from the head region along the concave ventral

surface of each. Gubernaculum simple. On each side of tail a narrow ala, arising just anterior to the heads of the spicules, becoming widest opposite the anal aperture, then gradually narrowing and uniting with body a short distance in front of tip of tail; point of attachment very variable. Free edge slightly crenate. Caudal papillæ absent.

EGGS. 0·07 mm. to 0·095 mm. long by 0·03 mm. to 0·035 mm. wide. Laid either unsegmented or segmented.

LARVÆ. Marcinowski (1909), p. 60–61 gives the following dimensions for the newly hatched larva, length, 0·38 mm.; breadth, 0·0115 mm.; œsophagus, 0·14 mm.; tail, 0·0423 mm.; stylet, 0·01 mm. The œsophagus is thus a little more than one third the total length. A well defined 2nd stage larva, such as occurs in *A. tritici*, is not found in this species, but growth takes place until a pre-adult stage is reached in which the sexes are differentiated. This is the infective stage which is resistant to desiccation and viable for $6\frac{1}{2}$ years.

LIFE HISTORY. All stages of the parasite, adults, larvæ and eggs, may be found in diseased material, and it is probable that more than one generation of adults occurs in a year. Rostrup (1926) showed that eggs may be laid at any time throughout the year. The present writer found that the time required for development from egg to sexually mature adult was from 24–30 days when clover seedlings were inoculated with eggs and later dissected to determine the presence of the worms.

Pre-adult larvæ, richly supplied with fatty food-reserves, form the infective stage, and it is worms in this stage of development which are produced in abundance in decaying narcissus bulbs, and which wander out at the broken edges of the basal plate. It is this stage also which is carried within the seed coats of composites and is thus ready to infect germinating seedlings.

GEOGRAPHICAL DISTRIBUTION. British Isles, France, Germany, Holland, Belgium, Norway, Sweden, Denmark, Austria, Czecho-Slovakia, Russia, Switzerland, Italy, Sicily, Algeria, South Africa, U.S.A., Canada, Argentina, Brazil, Australia, Hawaiian Islands.

HOSTS.

Gramineæ.

Agropyron repens (couch grass).
Anthoxanthum odoratum (sweet vernal grass).
Avena sativa (oats).
Dactylis glomerata (cocksfoot).
Holcus lanatus (Yorkshire fog).
Hordeum vulgare (barley).
Lolium italicum (Italian rye grass).
,, *perenne* (Perennial rye grass).
Poa annua (annual meadow grass).
Secale cereale (rye).
Setaria sp. (bristle grass).
Triticum vulgare (wheat).

Liliaceæ.

Allium cepa (onion).
,, *escalonium* (shallot).
,, *proliferum* (potato onion).
,, *schŏnoprasum* (chives).
,, *triquetrum* (triquetrous leek).
,, *vineale* (garlic).
Hyacinthus orientalis (hyacinth).
,, *romanus* (roman hyacinth).
Galtonia candicans (cape hyacinth).
Kniphofia "erecta" ? (red-hot poker).
Lilium grandiflorum.
Scilla campanulata (squill).
,, *cernua* (squill).
,, *nutans* (blue-bell, wild hyacinth).
,, *sibirica* (sibirian squill).
Tulipa Gesneriana (tulip).

Amaryllidaceæ.

Amaryllis formosissima (jacobean lily).
Galanthus nivalis (snowdrop).
Hymenocallis calanthina (sea daffodil of Peru).
Narcissus pseudonarcissus (daffodil).
,, *tazetta* (bunch flower narcis.)

Iridaceæ.

Gladiolus hybridus (gladiolus).
Iris xiphium (Spanish iris).

Orchidaceæ.

Disa grandiflora.

Polygonaceæ.

Polygonum convolvulus (black bindweed).
,, *fagopyrum* (buckwheat).
,, *lapathifolium* (knot-grass).
,, *persicaria* (persicaria).
Rheum rhaponticum (rhubarb).
Rumex acetosa (sorrel dock).

Urticaceæ.

Humulus lupulus (hops).

Chenopodiaceæ.

Beta vulgaris (mangold).
Chenopodium album (goosefoot).
Spinacia oleracea (spinach).

Caryophyllaceæ.

Dianthus barbatus (sweet william).
,, *caryophyllus* (garden pink).
,, *plumarius* (carnation).
Spergula arvensis (spurrey).

Begoniaceæ.

Begonia hybrida (tuberous rooted begonia).

Campanulaceæ.

Campanula persicifolia.

Ranunculaceæ.

Anemone japonica (Japanese windflower).
,, *spp.* ? (bulbous species).
Delphinium ajacis (annual larkspur).
,, *trollifolium* (wild larkspur)
Ranunculus acris (buttercup, crowfoot).
,, *repens* (creeping buttercup)

Cruciferæ.

Arabis alpina (alpine rockcress).
Brassica napus (rape).
,, *nigra* (black mustard).
,, *oleracea capitata* (cabbage).
,, ,, *sabauda* (savoy).
,, ,, *acephala* (kale).
,, ,, *gemmifera* (Brussel sprouts).
,, ,, *botrytis* (cauliflower).
,, ,, *gongylodes* (kohl-rabi).
,, *rapa* (turnip).
Camelina sativa (gold of pleasure).
Capsella bursa-pastoris (shepherd's purse).
Cardamine pratensis (cuckoo flower).
Cheiranthus allioni var. " moonlight."
,, *cheiri* (wallflower).
Isatis tinctoria (woad).
Lepidium sativum (garden cress).
Raphanus raphanistrum (wild radish).
Sinapis alba (white mustard).
,, *arvensis* (charlock).
Stenophragma thalianum (sand rocket).
Thlaspi arvense (penny cress).

Saxifragaceæ.

Saxifraga cotyledon.

Solanaceæ.

Nicotiana tabacum (tobacco).
Physalis pubescens.
Schizanthus retusus.
,, *wisetonensis.*
Solanum tuberosum (potato).
,, *villosum.*

Umbelliferæ.

Daucus Carota (carrot).

Compositæ.

Bellis perennis (common daisy).
Centaurea cyanus (cornflower).
,, *jacea.*
Cirsium arvense (creeping thistle).
,, *lanceolatum* (spear thistle).
Crepis taraxacifolia (beaked crepis).
,, *virens* (smooth crepis).
,, *fœtida* (fœtid crepis).
Cynara cardunculus (cardoon).
Hieracium Pilosella (mouse ear Hawkweed).
Hypochæris radicata (cat's ear).
Senecio vulgaris (groundsel).
Solidago canadensis (golden rod).
Sonchus asper (shaggy sow thistle).
,, *oleraceus* (common sow thistle)
Taraxacum officinale (dandelion).

Geraniaceæ.

Geranium molle (dove's foot geranium).

Linaceæ.

Linum usitatissimum (flax).

Cornaceæ.

Aucuba japonica (Japanese cornel).

Onagraceæ.

Œnothera Fraseri (evening primrose).
,, ,, var. *Youngii.*

Oleaceæ.

Syringa vulgaris (lilac).

Rosaceæ.

Fragaria chiloensis(Amer.wild strawb.).
,, *elatior* (hautboy).
,, *vesca* (European wild strawb.).
,, *indica* (Indian strawb.).

Leguminosæ.

Anthyllis vulneraria (kidney vetch).
Lathyrus odoratus (sweet pea).
Lupinus luteus (lupin).
Medicago sativa (lucerne, alfalfa).
Onobrychis sativa (sainfoin).
Phaseolus vulgaris (kidney bean).
Pisum arvense (field pea).
,, *sativum* (garden pea).
Trifolium incarnatum (crimson clover).
,, *pratense* (red clover).
,, *repens* (white clover).
Vicia faba (broad bean).
,, *sativa* (common vetch).

Primulaceæ.

Anagallis arvensis (scarlet pimpernel).
Lysimachia sp.
Primula japonica
,, *obconica* (top primrose).
,, *sinensis.*
,, *vulgaris* (primrose).

Convolvulaceæ.

Convolvulus arvensis (lesser bindweed).
Ipomea batatas (sweet potato).

Polemoniaceæ.

Phlox divaricata.
,, *Drummondii* (annual phlox).
,, *paniculata* syn. *decussata* (herbaceous phlox.
,, *suffruticosa.*

Scrophulariaceæ.

Calceolaria rugosa (yellow calceolaria).
Veronica serpyllifolia (speedwell).

Boraginaceæ.

Amsinckia intermedia.
Myosotis stricta.

Plantagineæ.

Plantago lanceolata (ribwort plantain).
,, *major* (greater plantain).
,, *maritima* (seaside plantain).

Dipsacaceæ.

Dipsacus fullonum (teasel, fuller's thistle).
,, *sylvestris* (wild teasel).

Bryophyta.

Hypnum cupressiforme (moss).

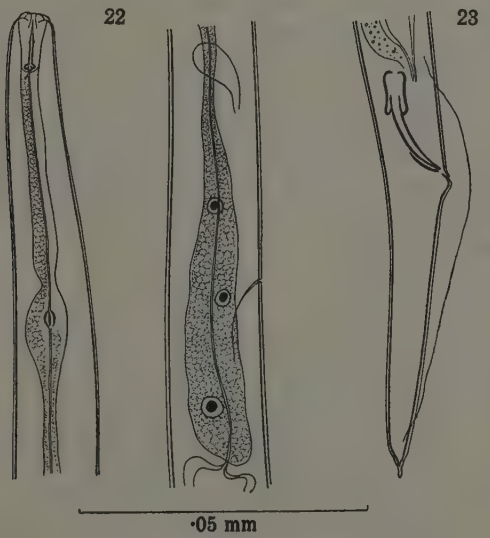
REFERENCES. 1, 2, 5, 7, 10, 31, 34-36, 39, 41, 42, 46, 56-58, 62, 66-70, 89, 91-93, 95, 96, 98, 101, 102, 105, 106, 110, 113, 116, 118, 119, 120.

ANGUILLULINA ANGUSTA (Butler, 1913) Goodey, 1932.

Syn. *Tylenchus angustus* Butler, 1913.

MORPHOLOGY. Dimensions :—*Female* : length, 0·7 mm. to 1·23 mm. ; breadth, 0·015 mm. to 0·022 mm. ; œsophagus, 0·14 mm. to 0·15 mm. ; tail, 0·045 mm. to 0·052 mm. ; stylet, 0·01 mm. ; $\alpha = 58–36$, $\beta = 8–7$, $\gamma = 20–17$, V = 80%. *Male* : length, 0·6 mm. to 1·1 mm. ; breadth, 0·014 mm. to 0·019 mm. ; œsophagus, 0·13 mm. to 0·14 mm. ; tail, 0·034 mm. to 0·048 mm. ; stylet, 0·01 mm. ; spicules, 0·02 mm. ; gubernaculum, 0·008 mm. ; $\alpha = 47–36$, $\beta = 7–6$, $\gamma = 23–18$.

In general structure and anatomy the adults are similar to *A. dipsaci*.



Anguillulina angusta.

Fig. 22. Œsophageal region, highly magnified.

Fig. 23. Male tail highly magnified, lateral view.

Body very slender, tapering but little anteriorly and posteriorly. Cuticle with fine transverse striations about 1·5μ apart. Head like a flattened disc, showing the six radial ridges ; no papillæ seen on it. Stylet typical, with three rounded basal swellings. Œsophagus of

usual structure; median bulb ellipsoidal, neck region rather slender, posterior part rather elongated containing three uni-nucleate œsophageal gland cells. Ducts from latter typical. Intestine, rectum and anus normal.

FEMALE. Ovary reaching almost to beginning of intestine, not reflexed but gradually widening backwards with ova in single file. At about 0·28 mm. in front of the vulva a constriction in the wall of the genital tube is found leading to the receptaculum seminis, this measures about 0·14 mm. long and is separated from the uterus by another constriction. There is a post-vulval uterine sac extending almost two-thirds of the distance from vulva to anus. Lips of vulva rounded and slightly protuberant. Tail almost cylindrical in shape but terminus suddenly tapering to a sharp pointed process.

MALE. Gonad anterior, single, extending sometimes almost to œsophagus; not reflexed. Rest of gonad practically as in *A. dipsaci*. Spicules paired and shaped as in *A. dipsaci* with anterior third expanded and rather oblong in outline, shaft tapering gradually to pointed tips. Gubernaculum simple. Caudal alæ arise a little in advance of heads of spicules and are inserted just short of the tip of the tail; they have faintly crenate edges. Tip of tail sharply pointed as in female.

EGGS. Butler gave 0·08 mm. to 0·084 mm. long by 0·016 mm. to 0·02 mm. wide.

LARVÆ. First stage larvæ measure about 0·17 mm. long and soon grow to 0·25 mm. Butler says an ecdysis occurs at about 0·25 mm. and another, probably the last, at about 0·6 mm.

LIFE HISTORY. Infection of the host takes place by worms climbing on to it from old diseased stubble and straw when atmospheric conditions are such that they can travel in films of moisture on the surface of the plant; they cannot migrate in dry air, but only when the relative humidity of the air is high. The normal parasitic life extends in the vast majority of cases from June to November and ceases before harvest. The species is ectoparasitic in habit and attacks the plant at the base of the peduncle, the stem just above the top node and that next below and within the glumes of the ear. Butler suggests that they continue to multiply on the plant and that at least three generations may be passed through between June and November. It has not been ascertained if one particular stage is the infective stage. It is considered

by Butler that infection is not seed borne.

HOST. *Oryza sativa* (rice).

GEOGRAPHICAL DISTRIBUTION. Ganges delta, East Bengal, Malaya.

REFERENCES. 8, 9, 61.

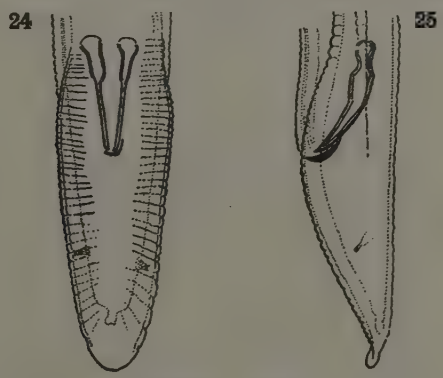
ANGUILLULINA MAHOGANI (Cobb, 1920) Goodey 1932.
Syn. *Tylenchus mahogani* Cobb, 1920.

MORPHOLOGY. Dimensions :—Cobb gives the following formulæ—

female $\frac{3.4 \quad 15. \quad 21. \quad {}^{60}\!-\!83\!-\!{}^{3} \quad 96.3}{3{\cdot}7 \quad 4{\cdot}8/ \quad 4{\cdot}8 \quad 4{\cdot}1 \quad 2{\cdot}3}$ 0.56mm

male $\frac{3.2 \quad 13. \quad 19. \quad {}^{67}\!-\!M \quad 94.8}{3{\cdot}2 \quad 3{\cdot}7/ \quad 4{\cdot} \quad 4{\cdot}4 \quad 2{\cdot}8_{1}}$ 0·52mm

Cuticle transversely striated, striæ about 1μ apart. Lateral fields about one-third width of body, winged with double contour. Head shaped like a flattened hemisphere, showing six radial surface ridges. Stylet typical, basal swellings only faintly tri-lobed and not prominent.



Anguillulina mahogani.

Figs. 24 and 25. Ventral and lateral views of male tail, × 1100. (After Cobb.)

Muscular bulb of œsophagus offset by a constriction in front and half as wide as body where it lies ; œsophagus then narrowing down so that

where the nerve ring crosses it, it is one-fifth the width of the corresponding region of the body. Œsophageal glands of the usual type present in posterior region. Intestine, rectum and anus normal.

FEMALE. Tail tapering somewhat to rounded terminus, a lateral innervated papilla present on each side about midway of its length. Gonad anterior, uterus containing one egg at a time laid in a segmented condition, a short post-vulval uterine sac present.

MALE. Lateral alæ rather narrow forming a somewhat inconspicuous bursa surrounding the tip of the tail, edge of alæ crenate. On either side a lateral papilla occurs situated a little more than halfway between the anus and the tip of the tail but not reaching the edge of the bursa. Spicules paired, from 0·018 mm. to 0·021 mm. long, sharply pointed, slightly concave ventrally, then expanding in the anterior half and with knobbed heads separated by a constriction from broadest part of shaft. Gubernaculum simple, about one-third length of spicules.

EGGS. As seen within uterus, about 0·046 mm. to 0·05 mm. long by 0·023 mm. wide.

LARVÆ. No particulars available.

LIFE HISTORY. Unknown. The species was found associated with a diseased condition in the tissues of mahogany trees.

HOST. Mahogany—genus and species not specified.

GEOGRAPHICAL DISTRIBUTION. Barbados, West Indies.

REFERENCE. 24.

ANGUILLULINA ARBORICOLA (Cobb, 1922) Goodey, 1932.

Syn. *Tylenchus arboricolus* Cobb, 1922.

MORPHOLOGY. Dimensions :—Cobb gives the following formulæ—

female $\frac{2.2}{1.9}$---$\frac{?}{2.9/}$---$\frac{8.}{3.4}$-----$\overset{70}{\frac{}{}}$$\frac{87.}{5.}$-------$\frac{?}{?}$ 0.7mm

male $\frac{2.2}{1.9}$---$\frac{?}{2.6/}$---$\frac{?}{?}$-------$\frac{M}{4.1}$---$\frac{95.7}{2.4}$ 0.7mm

Cuticle with very fine transverse striations ; striæ apparently crossing lateral fields. Head rather flat, narrower than body and offset by a

contriction, no papillæ seen. Stylet typical, basal swellings inconspicuous. Œsophagus typical, but with median bulb indistinct, no details given about the œsophageal glands and their openings as the material was not in a good condition. Intestine normal. Tail straight, conoid and having an acute point.

FEMALE. Ovary extending to œsophageal region and reflexed on itself anteriorly. Uterus containing one or two eggs at a time. Vulva elevated and rather conspicuous.

MALE. Testis single and outstretched anteriorly, forward end reflexed for a short distance on itself. Tail same shape as in female. Lateral alæ forming bursa almost surrounding tip of tail, edge faintly crenate; no caudal papillæ seen. Spicules paired, arcuate, strong and rather blunt, anteriorly expanded into heads. Some doubt as to presence of a gubernaculum.

EGGS. 0·078 mm. long by 0·039 mm. wide as calculated from particulars given by Cobb.

LARVÆ. No particulars available.

LIFE HISTORY. Unknown; worms found in blister-like structures on leaves. Cobb states that dried specimens of the worm do not revive in water, whereas examples of the next species do so readily.

HOST. *Fagus obliqua* (beech Roble).

GEOG. DIST. Santiago, Chile, S. America.

REFERENCE. 25.

ANGUILLULINA DURA (Cobb, 1922), Goodey, 1932.

Syn. *Tylenchus durus*, Cobb, 1922.

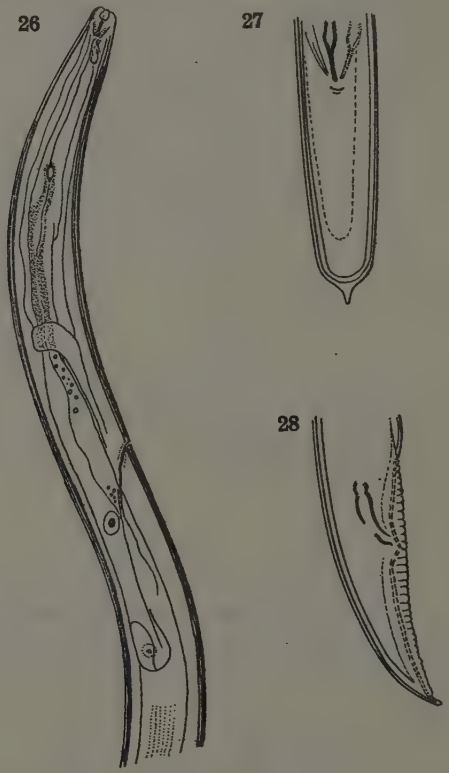
MORPHOLOGY. Dimensions:—Cobb gives the following formulæ—

$$female\ \frac{0.7}{1.1}\text{---}\frac{9.2}{2.2}\text{---}\frac{13.}{2.2}\text{---}\overset{60}{\text{---}}\frac{92.8}{2.7}\text{---}\frac{96.}{1.7}\ 0.82\text{mm}$$

$$male\ \frac{1.}{0.9}\text{---}\frac{10.7}{2.}\text{---}\frac{13.}{2.2}\text{---}\overset{55}{\text{---}}\frac{M}{2.7}\text{---}\frac{98.4}{2.}\ 1.0\text{mm}$$

Cuticle transversely striated, but striæ difficult to resolve. Lateral fields one-fifth to one-fourth body width, winged. Head convex-conoid, rounded and not offset by constriction. Six radial ridges only faintly discernible, head papillæ doubtful, faint traces only seen. Stylet typical

basal swellings not distinctly trilobed. Œsophagus typical, but median bulb inconspicuous and only half as wide as neck where it lies. Posterior region long and clavate containing œsophageal glands openings of which are typically situated. Intestine, rectum and anus normal. Tail tapering gradually to an acute convex-conoid terminus.



Anguillulina dura.

Fig. 26. Œsophageal region, lateral view, × 500.

Figs. 27 and 28. Oblique ventral and lateral view of male tail, × 500. (All after Cobb.)

FEMALE. Vulva conspicuous and massive; gonad anterior, uterus straight, ovary tapering anteriorly.

MALE. Lateral alæ arising gradually about 0·025 mm. in front of anus, forming a bursa having a crenate edge and almost enclosing the tail, the tip of which possibly is free. No caudal papillæ found. Spicules about 0·024 mm. long, strong, rather bluntly pointed with a slender shaft, heads knobbed by constriction. Gubernaculum simple, about one-third length of spicules.

EGGS AND LARVÆ. No dimensions given.

LIFE HISTORY. Unknown. Cobb says the worms have been taken from galls in the cortex of the trunk and branches of the chestnut oak. They can withstand prolonged desiccation and individuals will revive on re-moistening after being dried. It is not stated whether adults or only larvæ or both have this power.

HOST. *Quercus prinus* (chestnut oak).

GEOGRAPHICAL DISTRIBUTION. Virginia, U.S.A.

REFERENCE. 25.

ANGUILLULINA DARBOUXI (Cotte, 1912), Goodey, 1932.

Syn. *Tylenchus darbouxi*, Cotte, 1912.

MORPHOLOGY. Dimensions:—*Female*: length, 0·8 mm. to 1·55 mm.; width, 0·018 mm. to 0·045 mm.; stylet, 0·008 mm. to 0·01 mm. V = 65%–66%. Dimensions of male not given.

Head slightly offset, lip ridges probably typical. Stylet and œsophagus typical. Very few details are given by Cotte who says, however, that the species is closely related to *A. dipsaci* from which he thinks it originally descended. Gonads in both sexes presumably of the same general structure as in the two sexes of *A. dipsaci*. The male tail is without caudal alæ, but has spicules and a gubernaculum.

Micoletzky (1921) placed in this species three male worms, which lacked caudal alæ, discovered about the roots of grass at Cernowitz. They measured 0·635 mm. to 0·67 mm. long, and had the following proportions, $a = 41·3–37$, $\beta = 7·8–6·5$, $\gamma = 10–8·8$.

EGGS. 0·0875 mm. long by 0·033 mm. wide as estimated from Cotte's drawing.

LARVÆ. No particulars available.

LIFE HISTORY. Unknown. This species was found by Cotte in red, fusiform swellings on the stem of the host, having a width about twice that of the normal stem and in terminal rosettes of thickened leaves.

The parasite was located in the pith and in the outer part of the cortex.

HOST. *Thymus vulgaris* (wild thyme).

GEOGRAPHICAL DISTRIBUTION. Provence, France.

REFERENCE. 28.

ANGUILLULINA SYCOBIA (Cotte, 1920), Goodey, 1932.

Syn. *Tylenchus sycobius*, Cotte, 1920.

MORPHOLOGY. Dimensions :—Length, 0·45 mm. to 0·495 mm. ; width, 0·016 mm. to 0·017 mm. ; stylet, 0·02 mm. V = 75%.

Cuticle finely striated. Head with typical radial ridges. Cotte spoke of three lips, but this probably means three seen in one field and a total of six. They are also said to be somewhat more prominent than in *A. dipsaci*. Stylet rather large. Only one spicule seen, but a gubernaculum present and caudal alæ. The rest of the structure in both sexes practically the same as in *A. dipsaci*.

EGGS AND LARVÆ. No details available.

LIFE HISTORY. Unknown.

HOST. *Ficus* sp. ? (wild fig).

GEOGRAPHICAL DISTRIBUTION. Vaucluse, France.

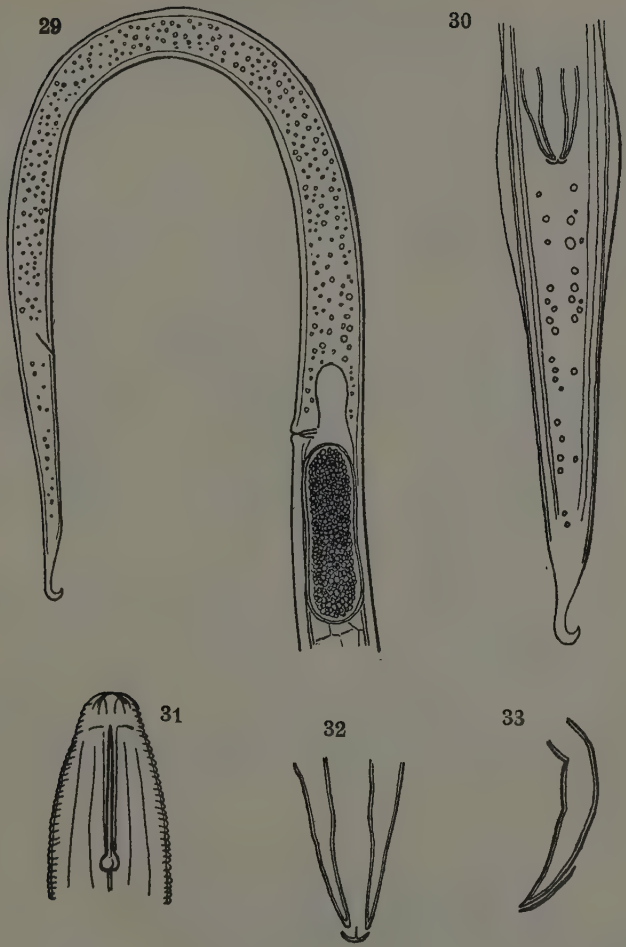
REFERENCE. 29.

ANGUILLULINA FUCICOLA (de Man, 1892), Goodey, 1932.

Syn. *Tylenchus fucicola* de Man, 1892.

MORPHOLOGY. Dimensions :—*Female* : length, 1·25 mm. to 1·45 mm.; width, 0·02 mm. to 0·03 mm. ; œsophagus, 0·2 mm. to 0·25 mm. ; stylet, 0·017 mm. to 0·018 mm. ; tail, 0·11 mm. to 0·12 mm. ; $\alpha = 50–45$, $\beta = 6–5$, $\gamma = 13–11$, V = 60%–64%. *Male* : length, 1·1 mm. to 1·25 mm. ; width, 0·018 mm. to 0·02 mm. ; œsophagus and stylet as in female ; tail, 0·1 mm. to 0·12 mm. ; spicules, 0·02 mm. to 0·025 mm. ; gubernaculum, 0·0075 mm. to 0·008 mm. ; $\alpha = 60–45$, $\beta = 6–5$, $\gamma = 13–11$.

Cuticle with fine transverse striæ. Lateral fields about one-third body width. Head cap-like, narrower than body and offset by slight constriction, also carrying fine transverse striæ. No distinct lips or papillæ but with the usual six radial surface ridges. In both sexes



Anguillulina fucicola.

Fig. 29. Hind region of female, lateral view, × 380.

Fig. 30. Male tail, ventral view, × 675.

Fig. 31. Head of female, lateral view, × 1350.

Fig. 32 and 33. Spicules and gubernaculum in ventral and lateral view, × 1350.

(All after de Man.)

the tip of the tail is constantly bent ventrally into a small hook which furnishes a good differential character. Excretory pore and canal well defined at one-eighth to one-ninth total body length from anterior end. Stylet typical with three basal swellings. Œsophagus with rather poorly defined median bulb and posterior glandular expansion. Intestine normal.

FEMALE. Gonad single, anterior end not reflexed, ovary separated from oviduct by slight constriction. Walls of oviduct and uterus composed of large polygonal cells. Vulva with rounded lips. Uterus with one egg at a time. A short post-vulval uterine sac present.

MALE. Gonad single, testis not reflexed anteriorly. Spicules paired, concave on ventral side, points sharp, shaft gradually broadening but anterior end not expanded and oblong in shape as in *A. dipsaci*. Gubernaculum shovel shaped, made up of two pieces joined in middle line. Lateral caudal alæ arising a little in front of anus and inserted about halfway down the tail.

EGG. Rather bean-shaped with rounded ends, one side concave the other convex; 0·08 mm. long by 0·026 mm. wide.

LARVÆ. No particulars given.

LIFE HISTORY. Unknown. Giving rise to galls on the thallus of the host as a result of which the latter is easily broken by waves, leaving stumps a few inches long bearing one or two clusters of galls.

HOST. *Fucus* (*Ascophyllum*) *nodosus*, a brown seaweed.

GEOGRAPHICAL DISTRIBUTION. East and West coast of Scotland, at Stonehaven and at the mouth of river Clyde, Ayrshire coast and Port Erin, Isle of Man. The last-mentioned site is added by the writer who is acquainted with material collected there in 1912.

REFERENCE. 79.

ANGUILLULINA DENDROPHILA (Marcinowski, 1909) Goodey, 1932.
Syn. *Tylenchus dendrophilus* Marcinowski, 1909.

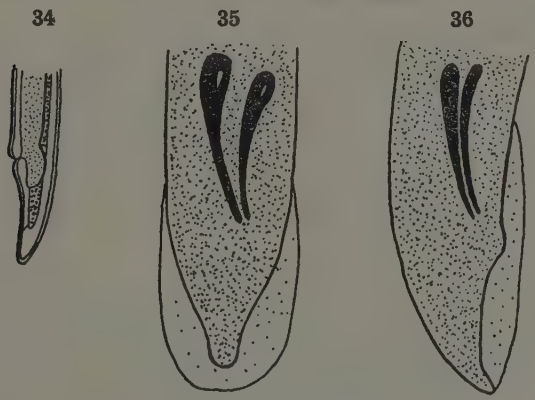
MORPHOLOGY. Dimensions:—*Female*: length, 0·97 mm.; width, 0·044 mm.; stylet, 0·005 mm.; $a = 24$, $\beta = 10$, $\gamma = 40$, V = 94·4%. *Male*: length, 0·81 mm.; width, 0·029 mm.; spicules, 0·022 mm.; $a = 30$, $\beta = 10$, $\gamma = 36·4$. The gamma proportion has been estimated in both sexes from Marcinowski's drawings. Cuticle with fine transverse striæ. Head slightly knobbed and narrower than body, scarcely offset

by constriction. Tail bluntly rounded and very short in both sexes. Stylet extremely short and basal swellings not clearly defined. Œsophagus typical, median bulb oval, terminal part not clearly defined. Anus not distinct in female.

FEMALE. Vulva placed very far posteriorly. Gonad single, outstretched anteriorly, front end not reflexed. A short post-vulval uterine sac present.

MALE. Spicules paired and comparatively long, no gubernaculum seen. Caudal alæ forming bursa surrounding tip of tail.

EGGS. Not seen.



Anguillulina dendrophila.

Fig. 34. Posterior end of female, lateral view, × 206.

Figs. 35 and 36. Ventral and lateral view of male tail, × 1155. (After Marcinowski.)

LARVÆ. First stage 0·36 mm. long, others seen about 0·4 mm. long having $a = 49$, their tails more pointed and elongate than those of adults.

LIFE HISTORY. Unknown. Marcinowski found adults and larvæ in the gum on a diseased cherry branch but was unable to determine whether the worms were causally related to the diseased condition. She attempted an inoculation of a cut healthy surface with some of the nematodes but they did not establish themselves in it. It is quite doubtful whether the species is parasitic or merely a free-living one

which found a congenial habitat in the gummy exudate from the diseased branch.

GEOGRAPHICAL DISTRIBUTION. Germany.

REFERENCE. 82.

PLANT-PARASITIC SPECIES ATTACKING ROOT STRUCTURES.

ANGUILLULINA RADICICOLA (Greeff, 1872) Goodey, 1932.

Syn. *Anguillula radicicola* Greeff, 1872.
Tylenchus radicicola (Greeff, 1872) Oerley, 1880.
Tylenchus hordei Schøyen, 1885.

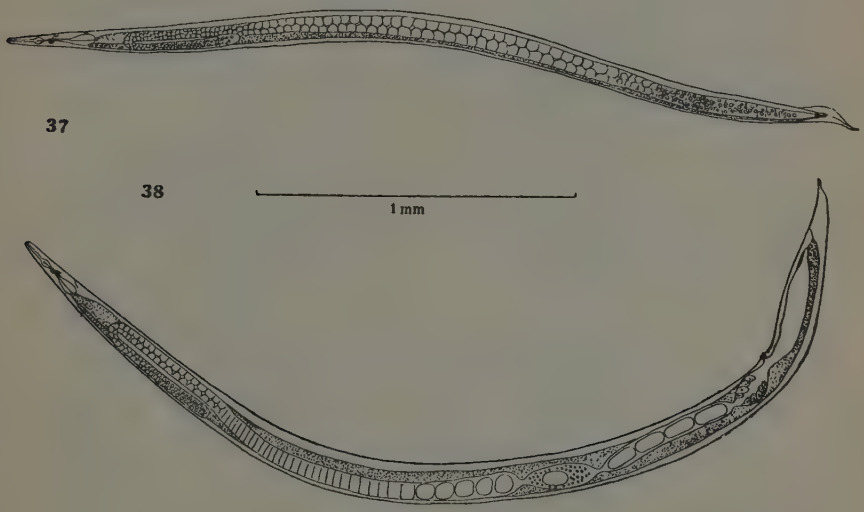
MORPHOLOGY. Dimensions :—*Female* : length, 1·22 mm. to 3·15 mm. ; width, 0·05 mm. to 0·12 mm. ; œsophagus, 0·16 mm. to 0·22 mm. ; tail, 0·09 mm. to 0·14 mm. ; stylet, 0·012 mm. to 0·016 mm. ; $a = 26–22$, $\beta = 13–9$, $\gamma = 20–18$, V = 77%–82%. *Male* : length, 1·2 mm. to 2·04 mm. ; width, 0·04 mm. to 0·07 mm. ; œsophagus 0·16 mm. to 0·22 mm. ; tail, 0·09 mm. to 0·11 mm. ; spicules, 0·033 mm. to 0·035 mm. ; gubernaculum, 0·012 mm. to 0·015 mm. ; $a = 30–24$, $\beta = 9–6$, $\gamma = 18–15$.

Adults of both sexes rather large and easily visible to naked eye, very variable in length. Body tapering anteriorly and posteriorly, terminus of tail in both sexes frequently shaped like a spear head and very sharply pointed. Cuticle transversely striated. Head cap-like, narrower than body and offset by constriction ; surface showing six radial ridges. Mouth terminal, leading to tubular buccal cavity about equal in length to the depth of the head. Stylet typical with three rounded basal swellings. Œsophagus typical, median bulb ellipsoidal, posterior glandular swelling pyriform. Openings of glands into lumen normal. Intestine very rich in large oil droplets, leading to anus by short rectum. Nerve ring crossing neck of œsophagus, excretory pore in vicinity of terminal region of œsophagus.

FEMALE. Gonad anterior, commencing in region of œsophagus and in its backward course frequently showing two distinct loops over the first part of the intestine. A constriction in wall of oviduct is followed by the swollen receptaculum seminis which is itself separated from the uterus proper by another constriction. Uterus a fairly long tube, capable of holding four to five eggs at a time, with walls composed of large cells.

Just anterior to the vulva the uterus swells out into an ampulla into the cavity of which the cells of the wall protrude. A large post-vulval uterine sac present, reaching almost to the end of the intestine. Lips of vulva rounded and often prominent.

MALE. Gonad single, anterior, testis commencing, as in female, close to œsophagus and doubly reflexed on itself over beginning of intestine.



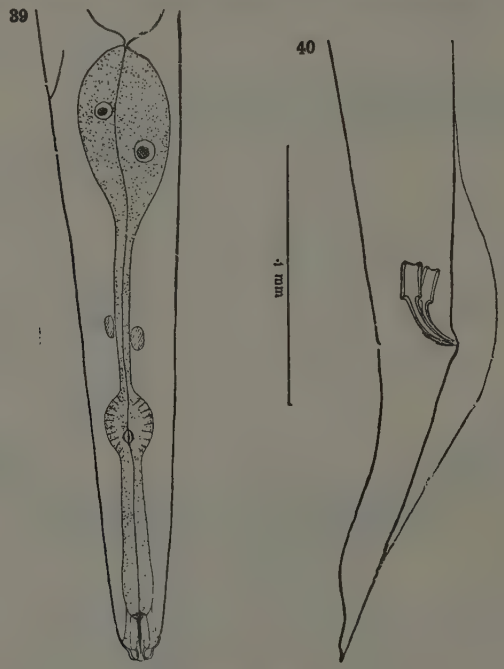
Anguillulina radicicola.

Figs. 37 and 38. Adult male and female respectively, lateral view.

Vas deferens well developed. Spicules paired, shaped almost exactly as in *A. dipsaci* but larger. Concave ventrally, points sharp, shaft gradually widening to expanded rather oblong heads. Gubernaculum simple. Caudal alæ arising about 0·08 mm. anterior to anus, widest opposite latter and inserted just in front of spear-like terminus of tail, edge crenate.

EGGS. Cylindrical with rounded ends; average size, 0·096 mm. to 0·098 mm. long by 0·038 mm. to 0·04 mm. wide. They may be as small as 0·07 mm. long by 0·038 mm. wide and as large as 0·15 mm. long by 0·04 mm. wide.

LARVÆ. First stage larvæ have the following dimensions :—0·45 mm. to 0·5 mm. long ; $a = 30–29$, $\beta = 7–4$, $\gamma = 7$. Kemner gave 0·3 mm. to 0·36 mm. long for larvæ hatching from eggs, so there is a good deal of variation possible. The first stage is the infective one. These larvæ



Anguillulina radicicola.

Fig. 39. Œsophageal region. Although only two nuclei of the œsophageal glands are shown, three are actually present. Fig. 40. Male tail, lateral view.

have sharply pointed tails, the stylet, œsophagus, intestine, nerve ring and excretory pore are all typical. The anus is frequently indistinct.

Goodey (1932a) found four ecdyses taking place in larvæ of about the following dimensions :—First ecdysis in larvæ 0·57 mm. to 0·59 mm. long, second ecdysis in larvæ 0·65 mm. to 0·68 mm. long, third ecdysis in larvæ 0·78 mm. to 0·8 mm. long, fourth and final ecdysis in larvæ

1·0 mm. to 1·32 mm. long for males and 1·0 mm. to 1·48 mm. long for females.

LIFE HISTORY. From the examination of galls on roots of *Elymus arenarius* and experimentally infected barley seedlings, Goodey (1932a) found that first stage larvæ invade roots on which galls are rapidly formed. Within the tissues the larvæ grow, undergoing four moults and becoming adults in from 18 to 21 days after invasion of the root. Egg-laying begins after another 10 to 12 days and continues for a considerable time since no free first stage larvæ were found within galls removed from roots 56 days from the beginning of the experiment; some newly hatched larvæ were found in galls after 64 days.

Disorganised galls without adults, larvæ or eggs were found on barley roots 56 and 64 days from the beginning of the experiment. With the breakdown of galls and the liberation of first stage larvæ, the normal course of the life history is completed. It is possible, though not probable, that a second generation of adult worms may be produced within one and the same gall.

Trail (1881) found that the parasite can withstand drying in galls on *Elymus arenarius* roots, and Thomson (1928) stated that larvæ can resume activity when galls, dried for two years, are soaked in water. Goodey (1932A) finds that only first stage larvæ become motile again when soaked out from dried galls; adults and developing larvæ do not revive.

HOSTS. The following plants, all members of the Natural Order Gramineæ, have been listed as hosts either under natural or experimental conditions.

Agropyron repens (couch grass) Natural Infection, *Aira flexuosa* (wavy hair grass) Expt. Inf., *Alopecurus pratensis* (meadow fox-tail) Nat. Inf., *Arrhenatherum avenaceum* (tall oat grass) Expt. Inf., *Avena sativa* (oats) Expt. Inf., *Elymus arenarius* (sea lyme grass) Nat. Inf., *Hordeum vulgare* (barley) Nat. Inf., *Phleum pratense* (timothy) Nat. Inf., *Poa annua* (annual meadow grass) Nat. Inf., *Poa pratensis* (smooth-stalked meadow-grass) Nat. Inf., *Secale cereale* (rye) Nat. Inf., *Triticum vulgare* (wheat) Expt. Inf.

GEOGRAPHICAL DISTRIBUTION. Germany, Sweden, Norway, Denmark, Finland, Scotland, England.

REFERENCE. 33, 43, 48, 49, 50, 51, 55, 63, 90, 104, 113A, 115, 117,

ANGUILLULINA SIMILIS (Cobb, 1893), Goodey, 1932.

Syn. *Tylenchus similis* Cobb, 1893.
Tylenchus acutocaudatus Zimmermann, 1898.
Tylenchus biformis Cobb, 1909.

The Burrowing Nematode.

MORPHOLOGY. Dimensions :—Cobb gives the following formulæ—

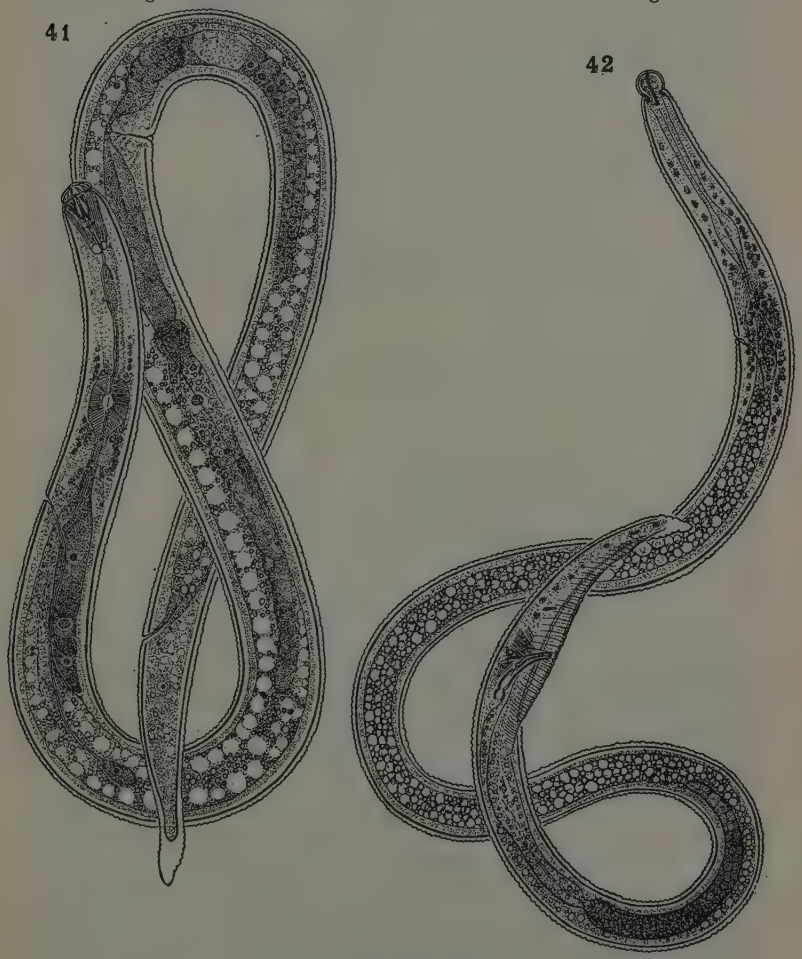
female $\left(\Longrightarrow \frac{3.}{2.5} - \frac{11.5}{3.2} = \frac{18.}{3.4} - \frac{59.^{38}}{3.8} - \frac{88.}{2.6}\right)$ .7mm

male $\left(\Longrightarrow \frac{2.4}{1.8} - \frac{12.}{2.6} = \frac{18.}{2.8} - \frac{M^{32}}{2.6} - \frac{89.}{2.2}\right)$ .7mm

Measurements are given by Godfrey (1931) which agree well with these ; he also gives the following proportions :—*Female :* $a = 28{\cdot}6$–$26{\cdot}6$, $\beta = 6{\cdot}9$–$6{\cdot}5$, $\gamma = 9{\cdot}1$–$8{\cdot}9$. V = 55·6%–58%. *Male :* $a = 29{\cdot}4$, $\beta = 6{\cdot}8$–$6{\cdot}7$, $\gamma = 8{\cdot}3$. Great sexual dimorphism is shown by this species.

FEMALE. Cuticle transversely striated ; striæ rather coarse, not crossing lateral fields : latter one-quarter to one-third width of body, having conspicuous wings which are slightly crenate where striæ meet them. Body tapering but little anteriorly. Head flattened and offset by slight constriction, six radial ridges on surface prominent, eight to ten very small transverse striæ also present on head. Head framework forming a buccal tube affording a guide for the stylet. Latter typical in structure, having three large basal swellings. Œsophagus typical ; anterior part about two-fifths width of body and constricted just in front of muscular bulb ; latter ellipsoidal, crescentic thickenings at centre prominent. Neck region narrow, crossed by nerve ring. Posterior glandular portion situated dorsal to beginning of intestine being rather less than half the width of the body here. The three uni-nucleate gland-cells arranged in line, one behind the other. Openings of glands into lumen of œsophagus typical. Intestine, rectum and anus normal. Tail tapering to blunt roughly conical terminus ; a small papillæ present on either side just short of the first third of the tail. Vulva slightly post-equatorial in position, gonads paired, opposed and comparatively short, terminal region of each ovary not reflexed. In between each uterus and ovary an almost spherical receptaculum seminis.

MALE. Body tapering anteriorly more than in female and the head offset by a deep constriction. Head practically hemispherical in shape and bearing minute transverse striæ. From Cobb's drawing it would



Anguillulina similis.

Figs. 41 and 42. Adult female and male, respectively in lateral view, × about 550. (From Muir & Henderson, after Cobb.)

appear that the radial lip ridges are not well marked.

Stylet very feebly developed and sometimes hardly visible. Lateral fields not so well developed as in female. Œsophagus rather ill-defined; median bulb elongate, posterior swelling not figured. Œsophageal glands apparently undeveloped. Intestine normal and well stocked with fatty globules. Tail tapering to blunt terminus having conical tip. Lateral alæ well developed arising slightly in front of heads of spicules and inserted quite close to tip of tail, edges crenate. A short lateral papilla on either side at about the anterior third of tail, not reaching edge of alæ. Spicules about 0·0205 mm. long, concave ventrally, points rather blunt, heads knobbed by constriction. Gubernaculum simple about 0·01 mm. long. Gonad single, rather short, testis ending well behind middle of body, not reflexed anteriorly. About one male to every eight or ten females.

EGGS. 0·053 mm. long by 0·0222 mm. wide, as calculated from Cobb's formula.

LARVÆ. No measurements available.

LIFE HISTORY. Young, probably first stage larvæ, enter roots and continue their development in the tissues where one generation follows another till such time as the root is broken down and rendered unsuitable for the continued existence of the parasite. Muir and Henderson (1926) found that a generation takes from four to five weeks under laboratory pot-culture conditions. Infestation may be very heavy and Cassidy (1931) has found as many as 2,532 examples of the parasite in one linear inch of affected sugar cane root. As a result of invasion by the parasite, cavities are formed in the cortex of affected roots and in these the worms appear to live.

HOSTS. *Ananas sativus* (pineapple), *Calpogonium mucunoides*, *Cajanus indicus* (pigeon pea), *Canna edulis* (edible canna), *Centrosema pubescens*, *Cyperus rotundus* (nut grass) *Coffea arabica*, *C. excelsa*, *C. robusta* (coffee), *Desmodium gyroides* (telegraph plant ?), *Gigantochloa apus* (bamboo), *Indigofera endecaphylla*, *Ipomea batatas* (sweet potato), *Musa sapientium* (banana), *Saccharum officinarum* (sugar cane) *Schizostachyum sp.* (bamboo), *Tephrosia candida*, *Thea sinensis* (tea), *Vigna Hosei*.

GEOGRAPHICAL DISTRIBUTION. Tropical and sub-tropical regions.

Fiji, Jamaica, Hawaiian Islands, Philippine Islands, Formosa, South India, Java and Dutch East Indies.

REFERENCES. 1a, 12a, 14, 17, 20, 38, 87, 121.

ANGUILLULINA PRATENSIS (de Man, 1881) Goffart, 1929.

Syn. *Tylenchus pratensis* de Man, 1881.
Tylenchus coffeæ Zimmermann, 1898.
Tylenchus penetrans Cobb, 1917.
Tylenchus brachyurus Godfrey, 1929.
Aphelenchus neglectus Rensch, 1924.

The writer has added two more species to the list of synonyms, namely *Tylenchus coffeæ* Zimmermann, 1898, and *T. brachyurus* Godfrey, 1929; the reasons prompting him to this course are discussed later in the section on systematics.

MORPHOLOGY. Dimensions:—*Female:* length, 0·47 mm. to 0·7 mm.; width, 0·021 mm. to 0·032 mm.; œsophagus, 0·1 mm. to 0·12 mm.; stylet, 0·015 mm. to 0·019 mm.; tail, 0·02 mm. to 0·022 mm.; $a = 30–20$, $\beta = 7–4·5$, $\gamma = 22–17$. V = 78%–83%. *Male:* length, 0·45mm. to 0·64 mm.; width, 0·02 mm. to 0·028 mm.; stylet, 0·013 mm. to 0·015 mm.; œsophagus, 0·1 mm. to 0·12 mm.; tail, 0·018 mm. to 0·02 mm.; spicules, 0·016 mm. to 0·0162 mm.; gubernaculum 0·005 mm.; $a = 29·3–22·5$, $\beta = 5–4·3$, $\gamma = 20–17·6$.

Body in both sexes comparatively stout, tapering but little anteriorly and posteriorly, tail of female broad and bluntly rounded. Cuticle with rather coarse transverse striæ. Head offset by constriction, cap-like and showing the six radial surface ridges very well developed and strongly cuticularised. Cuticle of head with fine transverse striæ.

Steiner (1927) has figured an end view of the head showing sub-ventral, sub-dorsal and lateral papillæ, the latter being the openings of the amphids. The writer has found fusiform amphidial pouches, one on each side of the stylet in a true lateral position; their narrow anterior extremities leading into the lateral regions of the head.

Cuticular ridges of head meet towards centre and form buccal tube about twice as long as depth of head and serving as guide to the stylet. Latter typical and rather large in both sexes, rounded basal swellings large and distinct. Œsophagus typical, a constriction of anterior portion immediately in front of muscular bulb. Latter rounded and

about three-fifths as wide as corresponding region of body. Posterior glandular portion lying obliquely ventral to beginning of intestine. The writer has found that in specimens examined in a fresh condition the three gland-cells are arranged in line as figured by Cobb for *T. penetrans*. The hindmost cell of the group is pointed distally. Openings from cells into lumen of œsophagus typical. Nerve ring, intestine, rectum and anus normal. Cobb figured the excretory canal connected posteriorly with a pyriform " renette " cell on the left side of the body close to the beginning of the intestine.

FEMALE. Tail tapering but little behind anus, tip bluntly rounded. Vulva with rounded, sometimes prominent lips ; vagina at right angles to ventral surface. Gonad single, anterior, front end of ovary not reflexed. A short post-vulval uterine sac present. Uterus containing one egg at a time.

MALE. Spicules paired, shaft making up about two-thirds total length, rather narrow ; points sharp. Anterior end expanded, tapering gradually to shaft ; gubernaculum simple. Gonad single, anterior, testis may be outstretched or have the front end reflexed. Caudal alæ forming bursa surrounding tip of tail, edge crenate. A single papilla on either side situated between half to two-thirds distance from anus to tip of tail, not reaching free edge of bursa but ending in a shallow depression on dorsal side of each wing. Widest part of bursa not wider than body.

EGGS. 0·063 mm. to 0·08 mm. long by 0·021 mm. to 0·025 mm. wide.

LARVÆ. First stage larva measured by Zimmermann was 0·22 mm. long by 0·01166 mm. wide.

LIFE HISTORY. Exact details of the life history are lacking but in all probability it is similar in essentials to that of *A. similis* with which it is often associated in the tropics. First stage larvæ probably act as the infective stage. Adults, larvæ and eggs may be found in parasitised roots and probably several generations are passed in one year. The worms make their way through root tissues, break down cell walls and feed on cell contents, bringing about a general destruction of cortical tissues of roots.

HOSTS. *Atriplex sp.* (Orache), *Avena sativa* (oats), *Beta vulgaris* (beet), *Brassica campestris* (rape), *B. oleracea* (cabbage), *Calpogonium mucunoides*

Cattleya sp. (orchid), *Centrosema pubescens*, *Cinnamonum camphora* (camphor), *Coffea arabica* (coffee), *Coffea robusta* (coffee), *Convallaria majalis* (lily-of-the-valley), *Daucus Carota* (carrot), *Dendrocalamus asper* (bamboo), *Dioscorea sp.* (yam), *Emilia sonchifolia* (red flowered pualele), *Ficus carica* (fig), *Fragaria chiloensis* (strawberry), *Gigantochloa apus* (bamboo), *Glycine hispida* (soy bean), *Gossypium sp.* (cotton), *Hordeum vulgare* (barley), *Latuca sativa* (lettuce), *Lathyrus odoratus* (sweet pea), *Linum usitatissimum* (flax), *Lupinus luteus* (lupin), *Lycopersicum esculentum* (tomato), *Medicago sativus* (lucerne), *Narcissus pseudonarcissus* (daffodil), *Nicotiana tabacum* (tobacco), *Papaver sp.* (poppy), *Phaseolus sp.* (bean), *Pisum sativum* (garden pea), *Populus sp.* (poplar), *Radicula Armoracia* (horse-radish), *Saccharum officinarum* (sugar cane), *Schizostachyum sp.* (bamboo), *Secale cereale* (rye), *Sinapis alba* (white mustard), *Sisyrinchium angustifolium*, *Solanum tuberosum* (potato), *Trifolium sp.* (clover), *Triticum vulgare* (wheat), *Vigna sinensis* (cow pea), *Viola sp.* (violet), *Weingärtneria canescens*, *Zea mays* (maize), various lawn grasses, species undetermined.

The foregoing list is mainly taken from that compiled by Goffart (1929) which includes all earlier records of plants parasitised by *A. pratensis*, *Tylenchus penetrans* and *Aphelenchus neglectus*. The writer has added to it coffee, Calpogonium, Centrosema, Dendrocalamus, Gigantochloa and Schizostachyum, as attacked by *T. coffeæ* of Zimmermann ; pineapple, tomato, cow-pea, soy-bean and red-flowered pualele from Godfrey, as parasitised by *T. brachyurus* ; and lettuce, daffodil, sweet-pea and lawn grasses based on his own observations.

SYSTEMATICS. Steiner (1927) showed that *Tylenchus penetrans* and *Aphelenchus neglectus* should be considered as synonymous with *T. pratensis*, it therefore remains for the writer to give reasons why he has included *T. coffeæ* Zimmermann, 1898 and *T. brachyurus* Godfrey, 1929 in the list of synonyms. *T. coffeæ* is discussed first.

Zimmermann, in his original paper, discussed the question of relationship of his species to *T. pratensis* and pointed out that, as measured by him, the worms from coffee roots were rather longer and broader than those described by de Man. He also thought that the tail of the male, as figured by de Man was less acute and provided with a larger bursa than that of the coffee root forms.

Goffart (1929) tabulated the points of similarity and difference between

the two species and, whilst suggesting that the very slight differences may be due to individual variation, concluded that the final decision of the matter must await the further examination of worms from coffee roots. Bally and Reydon (1931) suggest that *T. coffeæ* is probably synonymous with *T. penetrans* Cobb, 1917.

The writer considers that the dimensions and proportions of *T. coffeæ* as given by Zimmermann :—*Female* : length, 0·63 mm. to 0·68 mm. *Male* : length, 0·56 mm. to 0·61 mm. ; $a = 20{\cdot}83$ in female and 25·6 in male ; $\gamma = 20{\cdot}83$ in female, bring it within the dimensions of *A. pratensis*. The length of the stylet, 15μ and the relative distance of the vulva V = 81·2 per cent. agree with the corresponding dimensions found by the writer in specimens found in daffodil and grass roots.

In addition, the drawings given by Zimmermann of coffee root worms are so strikingly like *A. pratensis* in both sexes as to render the identity of the two species more certain. The writer, for instance, found a male of *A. pratensis* from grass roots presenting exactly the same appearance as that figured by Zimmermann in his fig. 10, where the tail is shown in ventral view and the anterior end of the testis is reflexed on itself.

The spicules as represented in his fig. 9 iv, though drawn on a very small scale, are quite recognisable as being shaped exactly like those of *A. pratensis*. The size of the egg as given by Zimmermann, namely 54μ by 25μ is shorter than the average dimensions for the egg of *A. pratensis* but as egg-size is very variable in this and other nematode species one would scarcely be justified in excluding *T. coffeæ* from *A. pratensis* on these grounds when all other morphological points reveal the identity of the two species.

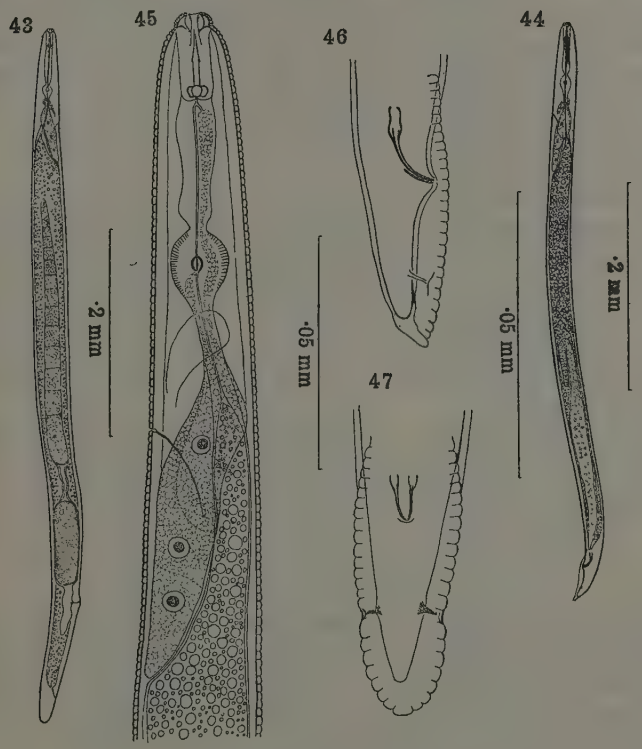
With regard to *T. brachyurus*, although recognising its close kinship to *pratensis*, Godfrey separated his species from it because of (1) the longer and more massive spear in *T. brachyurus*, (2) shorter proportional distance between vulva and end of tail, (3) consistently larger eggs, (4) lack of males.

Points one to three are, in the writer's view, covered by the variability shown by this species. The following comments on the matter are offered.

1. The stylet in *A. pratensis*, as revealed by the measurements of various workers, is rather variable in length, from 15μ to 19μ. Bovien (1929) gives it as 16μ to 19μ in the female. Hence we cannot admit a

stylet-length of 18μ to 19μ as of much value in support of a new species.

2. Godfrey gives V = 86%. Previous writers on *A. pratensis* give V as varying from 78 per cent. to 80 per cent. The writer has obtained



Anguillulina pratensis.

Figs. 43 and 44. Adult female and male in lateral view.

Fig. 45. Œsophageal region, lateral view, highly magnified.

Figs. 46 and 47. Lateral and ventral views of male tail, highly magnified. Spicules appear small in 47 owing to foreshortening. In all cases the appropriate scale lies to the right.

values ranging from 79 per cent. to 82·54 per cent., and is inclined to regard Godfrey's figure of 86 per cent. as an extreme value. At any

rate it seems scarcely reasonable to separate the two species on these grounds.

3. With regard to the dimensions of the eggs, Godfrey gives 80μ long by 38μ wide for *T. brachyurus*, stating that this is larger than for *A. pratensis*. Eggs of the latter are, however, very variable in size, as the following measurements show:—Cobb gives 78μ by 25μ, Rensch 63μ–68μ by 21μ–25μ, Steiner 67μ by 25μ. The writer has found eggs as small as 60μ by 21μ and as large as 80μ by 25μ. Consequently this feature cannot be considered as a good ground for excluding *T. brachyurus* from *A. pratensis*.

4. Absence of males. As Steiner pointed out in his paper, males have been of much rarer occurrence than females in all previous observations on this species. It is, therefore quite possible that, in spite of careful search for males, these may have escaped discovery by Godfrey in the case of diseased pineapple and other roots. In any case, absence of males can scarcely be admitted as a countervailing reason when the females show such close morphological similarity as to render their identity practically certain.

GEOGRAPHICAL DISTRIBUTION. England, Germany, Holland, Sweden Poland, U.S.A., Hawaii, Dutch East Indies, W. Africa, Mexico.

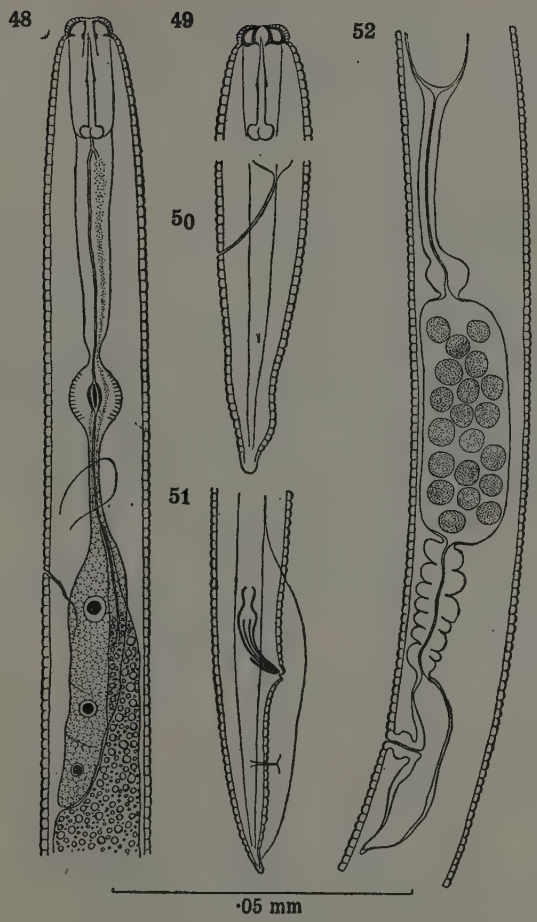
REFERENCES. 1a, 7a, 21, 37, 40, 77, 78, 97, 111, 121.

ANGUILLULINA MUSICOLA (Cobb, 1919) Goodey, 1932.

Syn. *Tylenchus musicola* Cobb, 1919.

MORPHOLOGY. Dimensions:—*Female*: length, 0·64 mm. to 0·68 mm.; width, 0·02 mm. to 0·025 mm.; œsophagus, 0·135 mm. to 0·14 mm.; stylet, 17μ; tail, 0·035 mm. $a = 32$–27, $\beta = 4{\cdot}8$–$4{\cdot}7$, $\gamma = 19{\cdot}4$–$18{\cdot}2$. V = 69%–75%. *Male*: length, 0·55 mm. to 0·57 mm.; width, 0·017 mm. to 0·02 mm.; œsophagus, 0·1 mm. to 0·12 mm.; tail 0·035 mm.; spicules, 0·015 mm.; gubernaculum, 0·005 mm.; $a = 32$–27, $\beta = 5$–$4{\cdot}8$, $\gamma = 16$–15.

In the structure of the head, shape and size of the stylet, structure and disposition of the œsophagus this species is so closely akin to *A. pratensis* that the description given of these anatomical features for that species may be taken as applicable to this. Adults of both sexes are, however, rather slenderer in *A. musicola* than in *A. pratensis*, and the tail in both sexes tapers much more in *A. musicola* than in *A. pratensis*.



Anguillulina musicola.

Fig. 48. Œsophageal region in lateral view.

Fig. 49. Head in surface view to show cuticular framework.

Figs. 50 and 51. Female and male tails, respectively in lateral view.

Fig. 52. Portion of female body in vicinity of vulva.

FEMALE. Gonad single, anterior, a short post-vulval uterine sac present as in *A. pratensis*. Vulva more anteriorly situated than in *A. pratensis*. One egg at a time in uterus. Tail tapering to a peg-like tip just anterior to which the dorsal side is first convex and then concave, whilst the ventral side is convex opposite the concavity of the dorsal side. A small lateral papilla present on either side about halfway down the tail.

MALE. Tail tapering considerably to a conical tip. Caudal alæ arising at about the level of the heads of the spicules and continued round the tip of the tail. Both Cobb and the present writer have stated that the bursa does not surround the tail, but a recent re-examination of the writer's mounted material revealed two males in ventral view which showed that the tip is completely enclosed by the bursa. A lateral view gives the impression that each wing joins with the body almost at the tip, the terminus of the tail being obscured. Spicules sharply pointed, shaft gradually widening to the broadest part, about three quarters the length from the tip, then slightly constricted and expanding again into a head. Gubernaculum about one-third length of spicules. A small lateral papilla on each side about two-thirds length of tail from anus.

The chief differences from *A. pratensis* are :—1. Slenderer body in both sexes. 2. Vulva more anterior. V = 69%–75% as against 78%–83% in *A. pratensis*. 3. Tail differently shaped in both sexes.

EGGS. Cobb gives 0·062 mm. long by 0·018 mm. wide for an egg seen in the uterus.

LARVÆ. No measurements available.

LIFE HISTORY. Unknown, but presumably similar to that of *A. pratensis*. The worms have been found associated with a soft rot in the roots of banana. Possibly one generation succeeds another till the tissues are no longer suitable for the continued growth of the parasites.

HOSTS. *Musa sapientium* ("bluggoe" banana), *Vitis vinifera* (grape vine).

GEOGRAPHICAL DISTRIBUTION. On banana, Barbados and Royal Botanic Gardens, Kew; Vine, Loomis, California.

REFERENCES. 22, 45, 111.

ANGUILLULINA CANCELLATA (Cobb, 1925) Goodey, 1932.

Syn. *Tylenchus cancellatus* Cobb, 1925.

MORPHOLOGY. Dimensions :—Cobb gives the following formula for the female, the male being unknown.

$$\textit{Female}\ \frac{3\cdot \quad 13\cdot \quad \cdot \quad 30\cdot \quad {}^{40}\!-\!68\cdot \quad 82\cdot}{2\cdot7 \quad 4\cdot \quad - \quad /4\cdot4 \quad 4\cdot4 \quad 2\cdot4} \quad 0\cdot5 \text{ mm.}$$

The only account of this species is contained in the descriptive lettering to the drawing of the worm. Head narrower than body, offset by a slight constriction, carrying fine transverse striæ. Cuticle of body with coarse transverse striations, the striæ carried on longitudinal ridges of which there are 16 towards the anterior end, 18 throughout the greater part of the body diminishing to 14, 10 and eight towards the posterior end. Tail long and tapering to a fine point. Stylet, œsophagus, nerve ring, excretory pore, intestine rectum and anus typical of the genus.

Vulva at 68 per cent. body length from anterior end, gonad single, anterior and without a post-vulval uterine sac.

EGGS AND LARVÆ. No information available.

LIFE HISTORY. Unknown. Cobb's drawing shows a worm rather closely resembling the free-living species, *A. agricola* de Man, which also has transverse striæ on the head and a well developed stylet. There is no evidence to show that *A. cancellata* is a pathogenic species, it may have been sheltering in the lesions on the pæony roots.

HOST. *Pæonia officinalis* (pæony). GEOGRAPHICAL DISTRIBUTION, U.S.A. REFERENCE. 26.

ANGUILLULINA ALATA (Cobb, 1930), Goodey, 1932.

Syn. *Tylenchus alatus* Cobb, 1930.

MORPHOLOGY. Dimensions :—Cobb gives the following formula—

$$\textit{male}\ \frac{5\cdot \quad 12\cdot \quad -19\cdot \quad {}^{74}\!-\!M. \quad 92\cdot8}{2\cdot5 \quad 3\cdot1/ \quad -3\cdot5 \quad 3\cdot5 \quad 2\cdot5} \quad 0\cdot53 \text{ mm.}$$

female unknown.

Cuticle with transverse striæ interrupted at lateral fields ; latter about quarter width of body and with rather strongly developed wings from which the specific name, *alatus*, has been taken. Head sub-hemispherical with about five fine transverse striæ. Offset from body by slight constriction. The usual six radial ridges apparently absent. Stylet long and typical, basal swellings prominent. Buccal tube extending backwards as guide for stylet. Œsophagus typical, median bulb ellipsoidal, œsophageal glands not well developed. Opening of dorsal gland typical just behind base of stylet. Intestine normal, well stocked with fatty food globules. Body tapering from some distance in front of anus to an acute or sub-acute terminus. Bursa well developed, arising well anterior to anus and barely including the tail, edge crenate. A small lateral papilla on either side about halfway down the tail, not reaching free edge of bursa. Spicules arcuate, points rather blunt, anterior ends very slightly expanded to form head. Gubernaculum simple, narrow, about half as long as spicules and closely underlying them. Anterior extent of testis uncertain.

EGGS AND LARVÆ. No particulars available.

LIFE HISTORY. Unknown.

HOST. *Cinchona succirubra* (cinchona).

GEOGRAPHICAL DISTRIBUTION. Belgian Congo.

REFERENCE. 27.

ANGUILLULINA PROCERA (Bally and Reydon, 1931).

Syn. *Tylenchus procerus* Bally and Reydon, 1931.

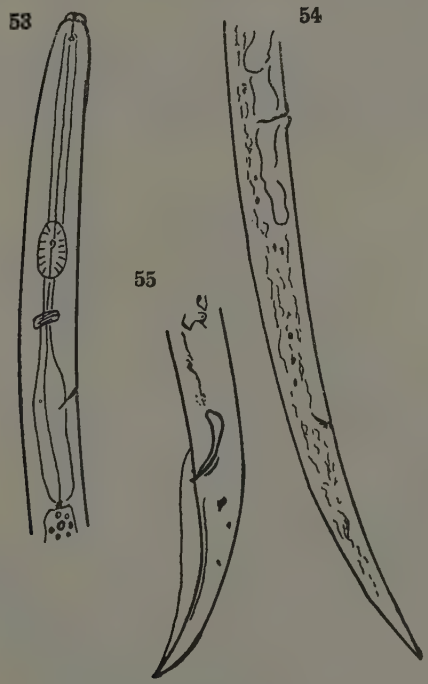
MORPHOLOGY. Dimensions :—Bally and Reydon give the following formulæ—

female, adult	1·3	10·7	19·2	80·8	93·0	0·67 mm.
	1·1	2·1	2·4	2·4	1·6	
male, not adult	1·8		23·2	50·0	89·3	0·418 mm.
	1·3		3·6	3·6	2·2	

Body slender, $a = 32·0$ to $41·3$, tapering but little anteriorly and considerably posteriorly to a sharp pointed tail without terminal process. Cuticle with faint transverse striæ. Head in form of a con-

spicuous frontal cap. Stylet weakly developed in both sexes. Œsophagus typical, median bulb with very small crescentic thickenings of lumen. Nerve ring and excretory pore normal in position.

FEMALE. Vulva about four-fifths body length from anterior end. Gonads given by Bally and Reydon as paired and opposed, the drawing



Anguillulina procera.

Fig. 53. Œsophageal region in lateral view, × 710.

Fig. 54 and 55. Female and male tail, respectively, lateral view, × 710. (After Bally & Reydon.)

of the female, however suggests an anterior ovary and a post-vulval uterine sac. In any case with the vulva so far posteriorly there would scarcely be room for a posterior ovary.

MALE. Caudal alæ well developed and reaching almost to tip of tail. Spicules with sharp points and heads rather knobbed. Gubernaculum simple, about one-third length of spicules.

EGGS AND LARVÆ. No particulars available.

OCCURRENCE. A doubtful parasite often found on the roots of *Coffea arabica* and *C. robusta* without causing remarkable damage. Dutch East Indies.

RELATIONSHIPS. From the dimensions and the shape as revealed by the drawings the species seems fairly closely akin to *A. intermedia*; it is, however, rather small for that species. The caudal alæ in extending almost to the tip of the tail differ from those of *A. intermedia*.

REFERENCE. 1a.

Free-living Species.

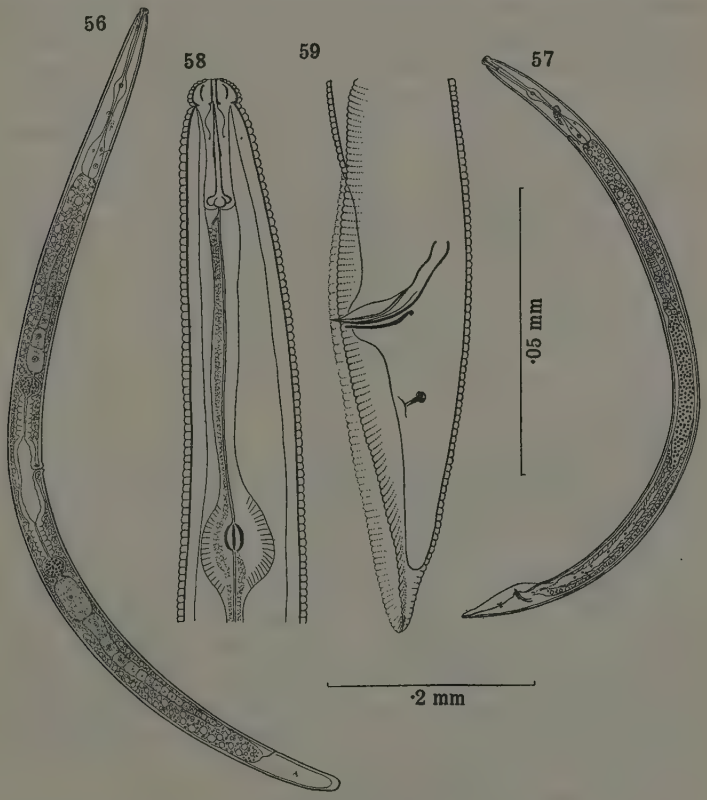
ANGUILLULINA DUBIA (Bütschli, 1873).

Syn. *Tylenchus dubius* Bütschli, 1873.
Tylenchus browni Kreis, 1929.

MORPHOLOGY. Dimensions:—*Female*: length, 0·6 mm. to 1·1 mm.; stylet, 19μ to 20μ long; $a = 30\text{-}27$, $\beta = 7\text{-}5$, $\gamma = 15\text{–}13$, V = 50%–55%. *Male*: length, 0·6 mm. to 0·9 mm.; spicules, 0·028 mm. to 0·03 mm.; gubernaculum, 0·01 mm. to 0·013 mm.; $a = 33\text{–}26$, $\beta = 6\cdot9\text{–}4\cdot7$, $\gamma = 15\cdot4\text{–}10\cdot3$.

Cuticle with fine transverse striations interrupted at lateral fields, latter about one-third width of body. Head distinctly offset by well marked constriction, narrower than body and practically hemispherical in shape. Cuticle of head with about eight fine transverse striæ. A marked feature of the species is the thick subcuticular layer, very hyaline in appearance, and occupying about one-seventh to one-sixth the width of the body on each side when viewed in optical section. The six radial ridges on head present but only seen after careful focussing under high magnification. Mouth terminal, leading to narrow buccal tube about as deep as head, here the wall bears lateral thickenings and is then continued backwards, being slightly convex and finally ending in a minute knob on either side. The structure has the appearance of a stylet guide. Stylet typical, anterior and posterior halves practically equal in length, former very sharply pointed,

latter with three distinct but not very large basal swellings. Stylet about one-seventh total length of œsophagus. Latter typical, anterior region rather narrow, median bulb oval or rounded with crescentic



Anguillulina dubia.

Figs. 56 and 57. Adult female and male, respectively, in lateral view.

Fig. 58. Head and front part of œsophagus, highly magnified, in lateral view.

Fig. 59. Male tail, lateral view. Horizontal scale applies to 56 and 57 and the upright scale to 58 and 59.

thickenings of lumen well developed, neck region long and narrow swelling out into the clavate, glandular terminal region. Œsophageal glands and their openings typical.

FEMALE. Vulva immediately post-equatorial; gonads paired, opposed and outstretched, ends of ovaries not reflexed. Between each uterus and ovary, oviduct swells to a spherical receptaculum seminis very similar in appearance to that figured by Cobb in *A. similis*. Tail practically cylindrical in shape, end bluntly rounded. A well-defined lateral papilla on each side a little in front of the middle of the tail.

MALE. Bursa large, completely enclosing tip of tail, edge finely crenate, arising well anterior to anus. Latter on a distinctly rounded prominence. Spicules paired, divergent, points very sharp, heads slightly expanded but open. A membranous ridge runs from the point of each to an attachment on ventral side about halfway down. Gubernaculum distinct, inner end slightly knobbed and upturned towards dorsal side of spicules. A lateral papilla on each side, not reaching edge of bursa, situated at about one-third the length of the tail from the anus. Gonad single, not reflexed anteriorly.

OCCURRENCE. Fairly frequently found in soil about the roots of cereals and grasses.

RELATIONSHIPS. Rather closely akin to *A. robusta* and *A. macrura* and other species the females of which have the vulva in the middle of the body but differing in the shape of the head, stylet, œsophagus and spicules.

Kreis (1929) described *Tylenchus browni* from preserved material taken from a street slope at Westtor, Peking, and the writer has given this as a synonym of *A. dubia*. The dimensions of the worms are as follows:—*Female*: 0·6656 mm. to 0·923 mm.; stylet, 15·6–20·8μ; $a = 53·6–35·4$, $\beta = 8·16–5·05$, $\gamma = 19·6–15$, V = 52%–57·6%. *Male*: 0·767 mm. to 0·8814 mm.; stylet, 13–20·8μ; $a = 47·6–36·9$, $\beta = 6·94–5·35$, $\gamma = 17·5–14$.

These dimensions and proportions agree very well with those given earlier for *A. dubia* except that they appear to be rather slenderer than *A. dubia*. The cuticle is coarsely striated, the sub-cuticular layer is thick, the head is almost hemispherical, the stylet is about the same length, the female gonads are double, opposed and outstretched and the female tail is bluntly rounded. In the male the bursa completely encloses the tip of the tail, the spicules, as figured, have the same shape but are a little shorter than in *A. dubia* and the gubernaculum has

the same shape as that of *A. dubia*. On all these points *T. browni* agrees with *A. dubia* from which Kreis separated it on account of its somewhat slenderer build, the shape of the spicules and the greater development of the bursa. None of these should, in the writer's opinion outweigh the points for inclusion indicated above. A feature not indicated by Kreis is the lateral caudal papillæ in both sexes, but possibly these would be difficult to distinguish in preserved specimens.

REFERENCES. 10, 64, 78.

ANGUILLULINA ROBUSTA (de Man, 1876).

Syn. *Tylenchus robustus* de Man, 1876.

Tylenchus dihystera Cobb, 1893.

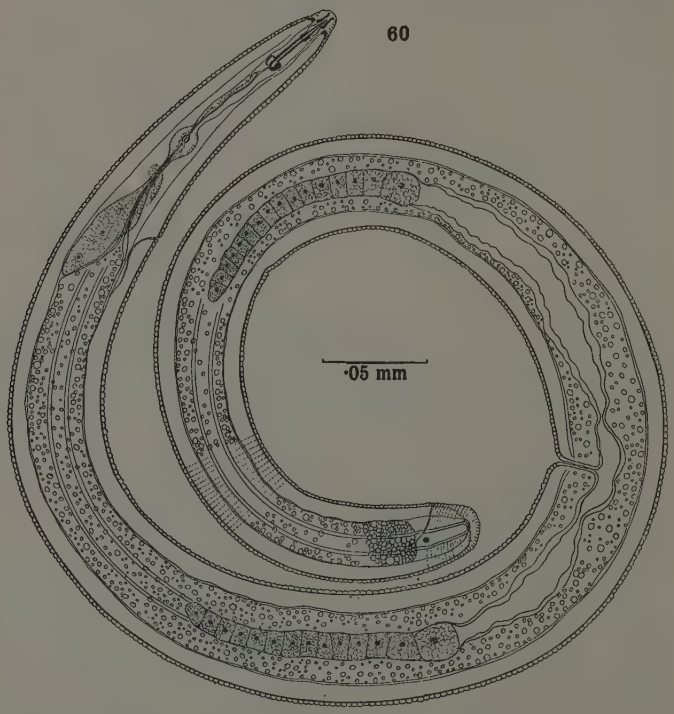
Tylenchorhynchus robustus var. *brevicaudatus* Micoletzky, 1921.

MORPHOLOGY. Dimensions :—*Female* : length, 0·85 mm. to 1·7 mm. ; stylet, 28–32μ ; $a = 40$–20, $\beta = 9{\cdot}7$–$4{\cdot}8$, $\gamma = 74$–35, V = 52%–65%. *Male* : length, 1·3 mm. ; $a = 35$, $\beta = 6$–5, $\gamma = 40$.

Cuticle very thick with coarse transverse striations, body tapering towards head but scarcely at all posteriorly, tail very short and bluntly rounded. Lateral fields well marked, about one-quarter body width. Head shaped like a truncated cone, offset from body by a very slight constriction and with a distinct crescentic thickening of the body wall curving inwards towards the buccal tube on either side at the level of the constriction. Cuticle of head also with transverse striæ closer than those on body. No distinct lips but towards centre of head the heavily cuticularised head framework forms a buccal tube with straight or slightly concave sides thickened a little at the mouth aperture. At the level of the posterior limit of the head the sides are again thickened and from this point backwards, in the region of the anterior half of the stylet, they form a lyre-shaped structure by first narrowing inwards and then gracefully curving outwards, with a final portion running parallel to the long axis of the stylet. Latter long and massive with thick walls, anterior conical half very distinct and clearly marked off from posterior half by a ring-like constriction. Basal swellings large and sometimes with rather flattened sides. Œsophagus typical, median bulb comparatively small, posterior glandular swelling generally somewhat pyriform. Openings of œsophageal glands typical,

outlet of dorsal gland sometimes rather a long way from base of stylet. Intestine as a rule richly stocked with fatty food globules. Rectum and anus distinct.

FEMALE. Vulva slightly post-equatorial in position, lips rounded and depressed, gonads paired, opposed and outstretched. Arising from each lateral field at about the level of the anus is a short papilla.



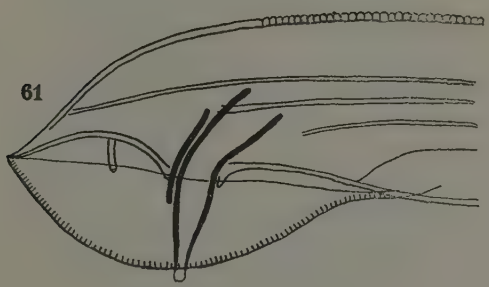
Anguillulina robusta.

Fig. 60. Young adult female, lateral view. Lateral fields and striations crossing body shown only to a limited extent.

MALE. de Man described the male which has a correspondingly short tail but perhaps not quite so short as that of the female. It is

completely enclosed by the bursa the wings forming which arise in front of the anus at a distance equal to the length of the tail. A single post-anal papilla present on each side a little in front of the middle of the tail. Spicules rather heavily built, points rather blunt and anterior ends open and expanded. Gubernaculum simple, rod-like, about one-third length of spicules.

OCCURRENCE. A slow moving species found around grass roots. de Man obtained his specimens from pasture and sandy dune soil washed by fresh or brackish waters. The writer has obtained specimens from around grass roots taken from heavy loam garden soil at this Institute.



Anguillulina robusta.

Fig. 61. Male tail, lateral view, highly magnified. (After de Man.)

On one occasion a fine adult female was taken from the stomach of a mole killed and dissected here. The male is less frequently found than the female.

RELATIONSHIPS. This species is the type of what may, for the sake of convenience, be termed the "*robusta*" group, comprising, *A. robusta*, *A. multicincta* and *A. macrura*. All three have the same shaped head, buccal tube and stylet, the latter being massive. *A. robusta* is distinguished by its size and the very short, bluntly rounded tail.

The writer has made *Tylenchus dihystera* a synonym since the account of its anatomy and particularly Cobb's statement that the stylet was

28μ long and had large basal swellings indicate its close kinship to *A. robusta*. Other points which support this are its length, the position of the vulva and the shape of the tail. Males were not seen and the worms were not figured.

REFERENCES. 15, 75, 78, 84.

ANGUILLULINA MULTICINCTA (Cobb, 1893).

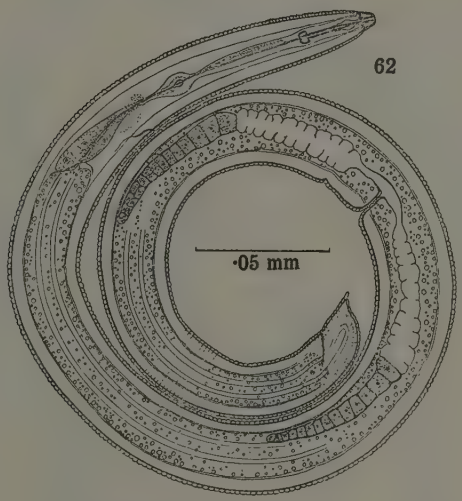
Syn. *Tylenchus multicinctus* Cobb, 1893.
Tylenchus erythrinæ Zimmermann, 1904.
Tylenchus olaæ Cobb, 1906.
Tylenchus pseudorobustus Steiner, 1914.
Tylenchus africanus Micoletzky, 1915.
Tylenchus spiralis Cassidy, 1930 (in litt.).
Tylenchorhynchus robustus var. *erythrinæ* (Zimmermann, 1904), Bally and Reydon, 1931.

MORPHOLOGY. Dimensions :—*Female:* length, 0·595 mm. to 0·86 mm.; stylet, 25–28μ, $a = 31·8–20·3$, $\beta = 7·6–5$, $\gamma = 54–33$, V = 57%–67%. *Male:* length, 0·47 mm. to 0·5 mm.; $a = 26·6–25$, $\beta = 6·3$, $\gamma = 33–20$.

Anatomically this species is practically identical with *A. robusta*. The cuticle is coarsely striated, the head is conical in shape and is offset by a slight depression, the buccal tube becomes lyre-shaped in the region of the anterior part of the stylet. The chief differences from *A. robusta* are (i.) its consistently smaller size, adult females are often only 0·6 mm. long, (ii.) the tail is not bluntly rounded, but carries a short ventral peg-like terminal process of rather variable length, (iii.) the vulva is generally a little more posteriorly situated than in *A. robusta*, (iv) lateral caudal papillæ pre-anal. The male has been figured by Cobb in his account of *T. multicinctus*, where it can be seen that the bursal wings surround the tip of the tail, that the spicules are comparatively stout and that a gubernaculum is present about one-third as long as the spicules. Lateral caudal papillæ are not shown, but they may have been overlooked.

OCCURRENCE. Around the roots of plants; Cobb found *T. multicinctus* around banana roots in Fiji and *T. olaæ* about the roots of diseased sugar cane in Hawaii. Zimmermann recorded *T. erythrinæ* from *Erythrina lithosperma* (dadap) roots in Java; Bally and Reydon from coffee roots. Cassidy has found *T. spiralis* commonly associated with roots of sugar

cane, pineapple, banana, rice and coffee in Hawaii. *T. pseudorobustus* and *T. africanus* were recorded from moss and algæ respectively. The writer has often encountered females of this species in washings from grass roots taken in various parts of the country; males have never been seen by the writer, and they must be of much less frequent occurrence than the females.



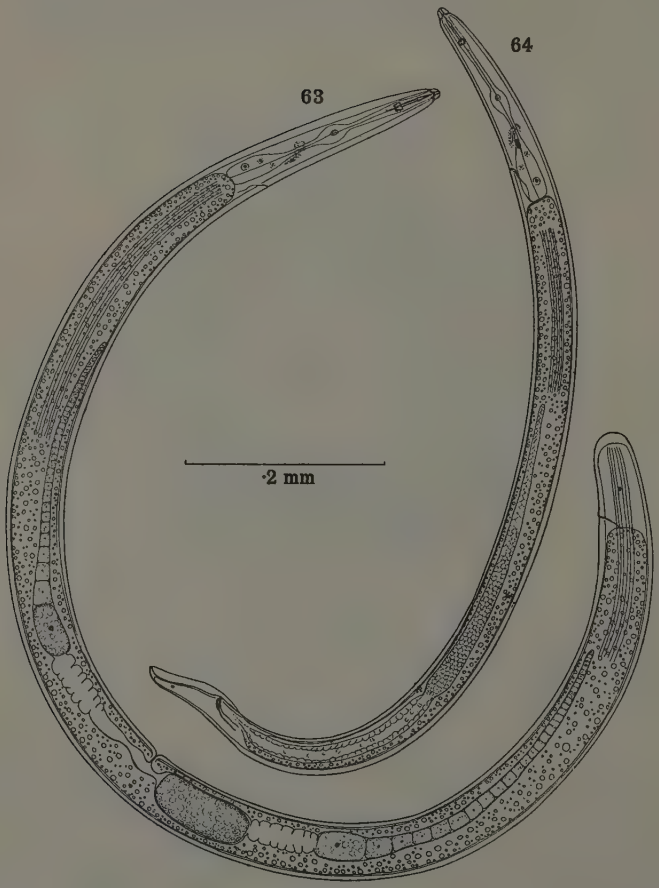
Anguillulina multicincta

Fig. 62. Young adult female, lateral view. Lateral fields and striations crossing body shown only to a limited extent.

RELATIONSHIPS. Very closely related to *A. robusta* and *A. macrura*. The five species which the writer has included as synonyms of *A. multicincta* all agree as to general size, the relative position of the vulva and the presence of the ventral peg-like caudal process. Where figures and sufficiently detailed descriptions are available they reveal the presence of the lyre-shaped buccal tube and a long stoutly built stylet. It is unfortunate that Cobb gave no figures of his *T. olaæ*.

REFERENCES. 1a, 12, 14, 16, 83, 84, 109, 122.

ANGUILLULINA MACRURA nom. nov. for
Aphelenchus dubius Steiner, 1914.

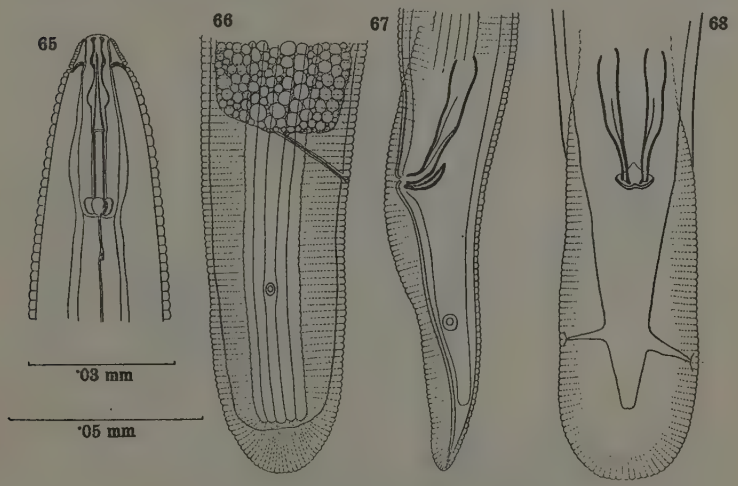


Anguillulina macrura.
Figs. 63 and 64. Adult female and male, respectively, lateral view.

MORPHOLOGY. Dimensions :—*Female :* length, 0·85 mm. to 1·68 mm.; stylet, 30–35μ ; $a = 31·1–22$, $\beta = 10·3–5·5$, $\gamma = 18·6–14$, V = 55%–57%. *Male :* length, 0·85 mm. to 1·77 mm. ; spicules, 0·035 mm. to 0·038 mm. ; gubernaculum, 0·009 mm. long ; $a = 37·5–24$, $\beta = 8·5–6·4$, $\gamma = 19·3–10·4$.

General and detailed anatomy as in *A. robusta*, but differing in having a comparatively long, almost cylindrical tail with a bluntly rounded tip. The male tail is also comparatively long.

FEMALE. Vulva only just post-equatorial in position, gonads opposed and outstretched. A lateral caudal papilla present on each side about half-way down the tail. The lateral fields are wide and show six longitudinal lines almost equidistant from one another.



Anguillulina macrura.

Fig. 65. Head in almost dorsal view, very highly magnified.

Fig. 66. Female tail, lateral view, highly magnified.

Figs. 67 and 68. Lateral and dorsal views, respectively, of male tail. The upper of the two scales applies to fig. 65 and the lower to the other figures.

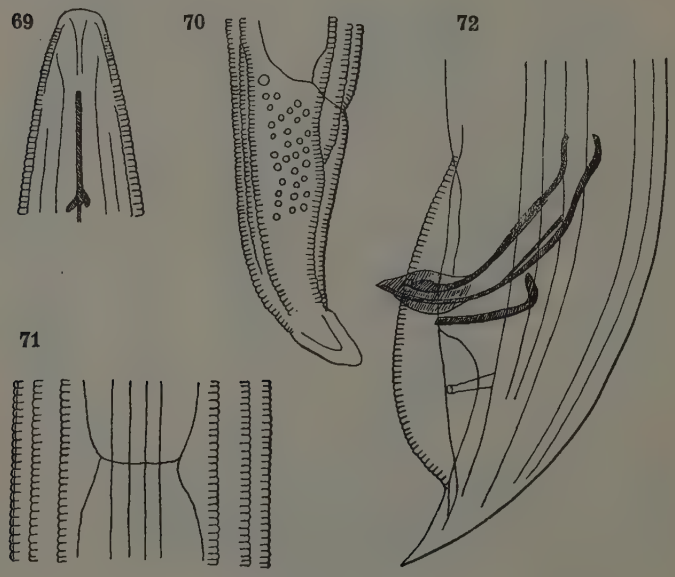
MALE. Bursa large, completely surrounding tip of tail, latter tapering and conical. A lateral papilla on each side, not reaching free edge of bursa, situated about two-thirds the length of the tail from the anus.

Spicules stout and gently curved, points rather blunt, open and rather thickened, shaft gradually widening to open expanded anterior end; a strengthening rib runs along the ventral surface from the points to about two-thirds the length. Gubernaculum, simple, triangular in outline when viewed dorsally, in lateral view rather boat-shaped with the inner end turned upwards towards the shaft of the spicule.

OCCURRENCE. Steiner recorded *Aphelenchus dubius* from dried arable soil. The writer has obtained specimens of both sexes on various occasions from washings of grass roots taken from garden and pasture soil at Winches Farm, males being practically as frequent as females.

RELATIONSHIPS. Very closely related to *A. robusta*, but clearly distinguished from it by the longer tail in both sexes and by the lateral fields.

REFERENCE. 109.



Anguillulina lamellifera.

Figs. 69 and 70. Head and tail of female.

Fig. 71. Surface view over end of œsophagus.

Fig. 72. Male tail, lateral view. All highly magnified. (After de Man.)

ANGUILLULINA LAMELLIFERA (de Man, 1880).

Syn. *Tylenchus lamelliferus* de Man, 1880.

MORPHOLOGY. Dimensions :—*Male* and *female* 1 mm. long, $\alpha = 27$–25 in both sexes, $\beta = 6$ in female, 5·5 in male, $\gamma = 21$–18 in female, 26 in male. V = 51·2%. This species is distinguished by the presence of longitudinal membranes or lamellæ of the cuticle which also carry very fine transverse striæ. Body tapering in the œsophageal region to the head which is conical in shape and not offset by constriction. Stylet delicate and thin, but basal swellings distinct, and having a length equal to about one-sixth the distance from the mouth aperture to the beginning of the intestine. Œsophagus typical, with moderately large median bulb and broad posterior swelling.

FEMALE. Vulva immediately post-equatorial in position ; gonads paired, opposed and outstretched. Tail conical and with rounded tip.

MALE. Caudal wings forming bursa surrounding tip of tail, a post-anal papilla on each side a little in advance of the middle of the tail. Spicules stout, as figured by de Man (1884), Pl. XXII., 94d, reminding one of those of *A. macrura*. Gubernaculum simple with inner end bent upwards towards spicule.

OCCURRENCE. A slow moving species from damp sandy pasture soil around grass roots in Holland.

RALATIONSHIPS. Rather close to *A. robusta* and *A. macrura*, but differing in the buccal tube and in having a delicate stylet.

REFERENCES. 76, 78.

ANGUILLULINA OBTUSA (Bastian, 1865).

Syn. *Tylenchus obtusus* Bastian, 1865.

MORPHOLOGY. Dimensions :—Bastian gave the following : *Female :* length, 0·8 mm. ; width, 0·033 mm. ; tail, 0·0584 mm. ; stylet, 17·7μ, $\alpha = 26$, $\beta = 5$, $\gamma = 15$, V, ? " near commencement of posterior third of body." *Male :* length, 0·769 mm. ; width, 0·033 mm. ; tail, 0·0508 mm. ; spicules, 25·4μ ; gubernaculum, about 12μ.

He said that the body tapers very slightly anteriorly, and still less posteriorly where it is blunt and rounded. Head rather truncate. Œsophagus about one-fifth total length, not one-fourteenth as given by Bastian,

obviously in error, as his fig. 117 proves.

The writer has found, in washings from grass roots, two young adult female worms which he considers belong to this species : their dimensions were as follows : length, 0·68 mm. and 0·66 mm. ; stylet, 20μ ; a = 26·5 and 23, β = 4·8 and 4·2, γ = 14 and 13·8, V = 58·5% and 56·2%.

They have a shorter length than Bastian gives, but agree well with the proportions calculated from his measurements. Cuticle with rather coarse striations. Head somewhat flattened, rounded and carrying about six small transverse striæ. Cuticular head framework strongly developed, showing six radial surface ridges and yellowish in colour by transmitted light. Buccal tube swelling out a little in region of front half of stylet. Latter stout and massive with large rounded basal swellings. Œsophagus typical ; median bulb round, posterior glandular region broad and clavate containing three large nuclei. Intestine well stocked with fatty food globules. Tail tapering very slightly to a blunt terminus which agrees well in general shape with that shown by Bastian in his fig. 118. In the writer's specimens the striæ did not continue round the tip of the tail, but the cuticle here was irregularly lobed, as shown in fig. 75.

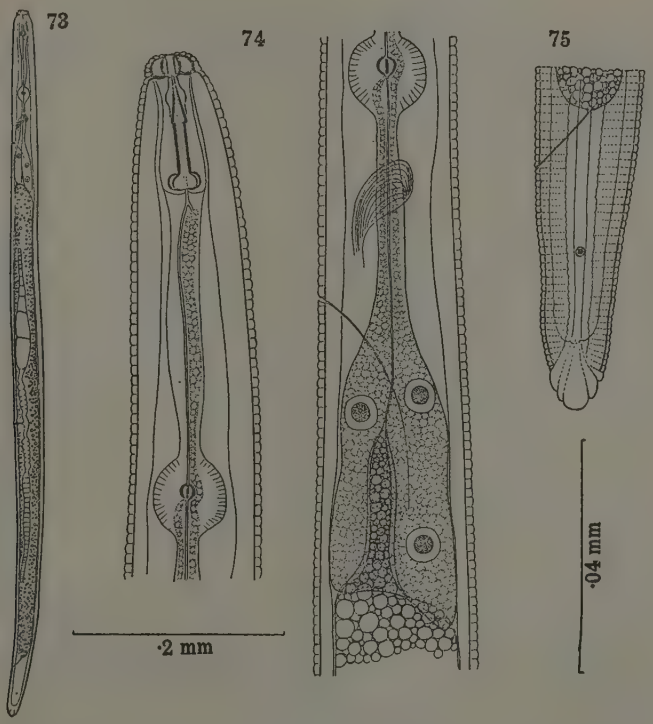
A lateral caudal papilla present at the centre of each lateral field about halfway down the tail. Vulva a little post-equatorial in position, whereas Bastian says, " near the commencement of the posterior third of the body." This is far from precise, and it is possible that in older and larger specimens the vulva would be located more posteriorly. Gonads paired, opposed, the ovaries not being reflexed.

MALE. Bastian says that the caudal alæ are transparent and extend on either side from a little above the anus to posterior extremity. His fig. 118A, small as it is, gives the appearance of having the bursa completely enclosing the tip of the tail. Unfortunately, the writer so far has not succeeded in finding male examples of this species.

OCCURRENCE. Bastian's material was from sandy soil about oat roots, and the writer's specimens were obtained from around grass roots taken in the garden at Winches Farm.

RELATIONSHIPS. From the particulars supplied by Bastian, very obscure. If the writer has correctly classified his specimens then the species is fairly closely related to *A. dubia*, *A. robusta*, and the other species having the vulva just post-equatorial in position and paired

opposed ovaries. It differs from the two species mentioned in the shape of the head the cuticular framework of which closely resembles that of *A. pratensis* and *A. musicola*. At first sight it is easily confused with



Anguillulina obtusa.

Fig. 73. Young adult female, lateral view. Horizontal scale on left.
Fig. 74. Head and œsophagus shown in two portions, lateral view.
Fig. 75. Female tail, lateral view.

A. pratensis both in head structure and shape of stylet, but closer examination shows that the stylet is more massive than in that species, that the vulva is not posteriorly placed and that the tip of the tail is differently shaped.

REFERENCE. 2.

ANGUILLULINA GRACILIS (de Man, 1880).

Tylenchus gracilis de Man, 1880.

MORPHOLOGY. Dimensions :—de Man gave the following : *Female :* length, 2·2 mm. or a little longer ; $a = 70–65$, $\gamma = 18$. *Male :* length, 2·1 mm. ; $a = 70–65$, $\gamma = 20$. Imamura (1931) gives *Female :* 2·75 mm. to 3·53 mm. ; $a = 85–72·3$, $\beta = 35·3–22·9$, $\gamma = 27·6–24·2$, V = 49·4%–58·6% ; *Male :* 2·25 mm. to 3·21 mm. ; $a = 83·1–75$, $\beta = 32·1–21·3$, $\gamma = 26·3–22·5$.

This species is remarkable for its great length and slenderness. Cuticle with fine transverse striations. Head slightly offset, rather low, convex anteriorly. Cuticular head framework well developed and radial surface ridges present. Stylet stout and with large rounded basal swellings, about one-fifth the distance from anterior end to far side of median œsophageal bulb. Latter rather large, posterior glandular swelling indistinct. Excretory pore a little behind median œsophageal bulb. Intestine having a fine granular structure.

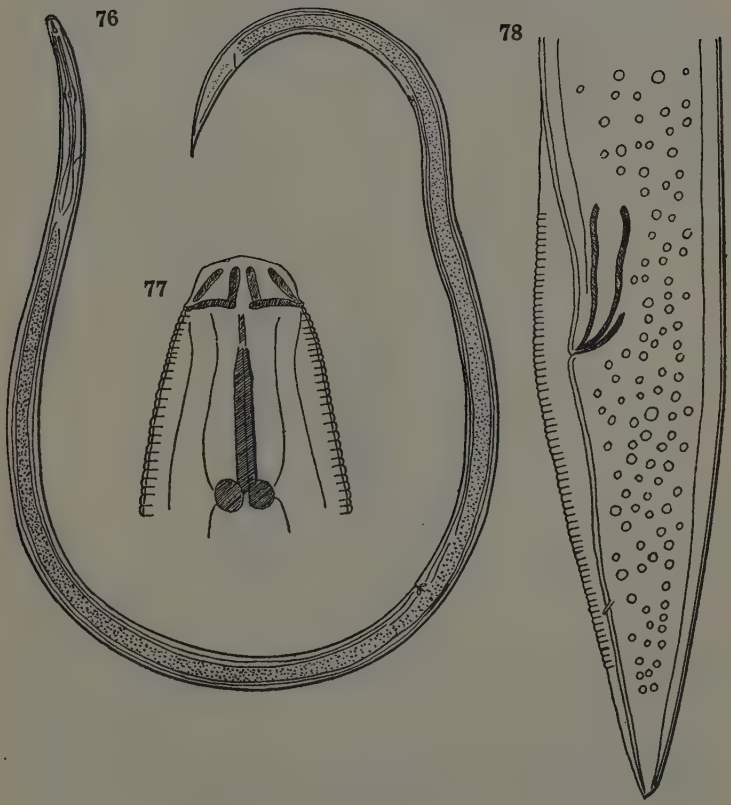
FEMALE. Vulva practically equatorial or immediately post-equatorial in position, gonads paired, opposed and outstretched. Tail tapering gradually to a pointed tip.

MALE. Tail conical as in female with pointed tip, but with bursal wings completely enclosing terminus. A lateral papilla on each side a little behind the middle of the tail. Spicules rather small and stout, points sharp, anterior ends rather broad and expanded. Imamura shows the head end of the spicule rather knobbed. Gubernaculum simple.

OCCURRENCE. A slow moving species, rarely seen according to de Man, from moist woodland and pasture soils, Holland. Imamura found 92 females and 25 males in soil from a paddy field at Komaba, Tokyo, Japan.

RELATIONSHIPS. Rather distantly related to *A. dubia* and *A. robusta* in having the vulva equatorially placed but distinguished by great length and slender build.

REFERENCES. 60, 76, 78, 86.



Anguillulina gracilis.

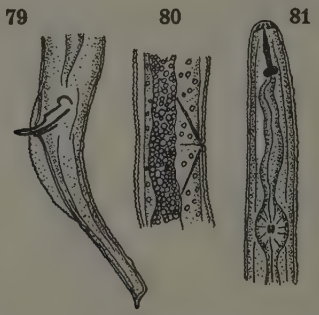
Fig. 76. Female, lateral view, × 125.
Figs. 77 and 78. Head and male tail, highly magnified. (All after de Man.)

ANGUILLULINA APAPILLATA (Imamura, 1931).

Syn. *Tylenchus apapillatus* Imamura, 1931.

MORPHOLOGY. Dimensions :—*Female :* length, 1·17 mm. (0·93 mm. to 1·5 mm.) ; $a = 55$ (60–50), $\beta = 20·3$ (25–17·4), $\gamma = 17·7$ (25–16·3), V = 53·3% (50·5%–58%). *Male :* length, 1·7 mm. (1·02 mm. to 1·32 mm.) ; $a = 53·3$ (53·7–52·8), $\beta = 22·1$ (24·3–21·1), $\gamma = 20·8$ (21·3–20·4).

Body very slender, tapering towards both ends. Cuticle thin, transparent, colourless, with fine transverse striæ. Lateral field winged, running almost entire length of body. Head almost hemispherical and with the usual six radial ridges connected with cuticular head framework serving as stylet guide. Stylet strong and with distinct



Anguillulina apapillata.

Figs. 79, 80 and 81. Male tail, region of vulva and anterior end, respectively. (After Imamura.)

tri-lobed basal thickenings, œsophagus typical, median bulb oval, posterior part indistinct. Excretory pore some distance behind median bulb. Intestine well stocked with fatty food globules.

FEMALES. Vulva slightly post-equatorial in position, ovaries opposed and outstretched. Tail tapering to a point but a little longer than in the male.

MALE. Gonad single, running anteriorly. Spicules rather slender, heads knobbed, points sharp. Gubernaculum simple and about one-third as long as spicule. Caudal alæ arising at about the level of heads

of spicules and joining body again about halfway down the tail. Caudal papillæ absent. The tail, as figured by Imamura has a small, pointed process at the tip.

OCCURRENCE. In soil of a paddy field at Komaba, Tokyo, Japan, Imamura found 33 females and seven males as well as 16 larvæ.

RELATIONSHIPS. Considered by Imamura to be closely related to *A. gracillis* but differing in its smaller size, in the bursa not enclosing the tip of the tail and in the absence of caudal papillæ in the male.

REFERENCE. 60.

ANGUILLULINA SYMMETRICA (Cobb, 1914).

Syn. *Tylenchus symmetricus* Cobb, 1914.

MORPHOLOGY. Dimensions :—Cobb gives the following formulæ—

Female	2·7	10·8	17·0	—49— (60)	90·2	0·7 mm.
	1·4	2·8	3·3	3·8	2·7	
Male	3·1	13·5	20·5	—M— (53)	89·1	0·6 mm.
	2·2	3·6	3·9	4·2	3·2	

Cuticle rather thick with transverse striæ. Lateral fields one-fourth to one-fifth width of body. Head offset by very slight constriction, somewhat rounded, no distinct lips. Stylet typical, basal thickenings distinct. Œsophagus typical. Tail conoid and tapering in final region to very fine point.

FEMALE. Vulva practically equatorial in position. Gonads paired, opposed and outstretched. One egg at a time in uterus.

MALE. Tail same shape as that of female. Caudal alæ not large but fairly well developed and not extending beyond ventral contour of body, arising a short distance in front of anus and joining body again about halfway between anus and tip of tail. A single post-anal papilla on each side.

OCCURRENCE. In black clay with much decaying vegetation at Arlington, Virginia, U.S.A.

RELATIONSHIPS. Very obscure; unfortunately no drawings are given by Cobb.

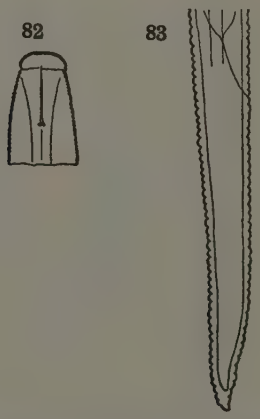
REFERENCE. 19.

ANGUILLULINA TENUIS (Micoletzky, 1921).

Syn. *Tylenchus tenuis* Micoletzky, 1921.

MORPHOLOGY. Dimensions :—The species was described from two females only ; male unknown. Length, 0·69 mm. ; $\alpha = 41·7$, $\beta = 3·8$, $\gamma = 11·2?$, V = 52% ; anterior ovary, 24% ; posterior ovary, 23% ; stylet, 20% of œsophageal length, egg, 0·038 mm. by 0·01 mm.

Body slender, tapering towards each end. Cuticle with fine transverse striæ, latter about 1·5μ wide in middle of body and 0·7μ towards anterior end. Lateral field distinct, about one-fourth width of body.



Figs. 82 and 83. *Anguillulina tenuis*. Head and tail of female. (After Micoletzky.)

Head rather weakly offset, cap-like with convex sides, no papillæ seen. Stylet very delicate, weakly knobbed basally. Œsophagus very long and with elongated bulbs, posterior swelling clearly marked off from intestine. Latter with numerous granules. Rectum longer than body diameter at anus, anus indistinct. Vulva practically equatorial in position, gonads paired, opposed. Tail but little narrower than body, tapering to a conical tip.

OCCURRENCE. Very rare, in alpine mosses. Steiermark, Austria.

RELATIONSHIPS. Micoletzky placed it close to *A. uniformis* Cobb,

from which it differs in the shape of the tail, in its longer œsophagus, in having the vulva more posteriorly placed, in having the head offset and in having a shorter stylet. It differs from *A. dubia* in having a much longer œsophagus and in the conical tail.

REFERENCE. 84.

ANGUILLULINA CLAVICAUDATA (Micoletzky, 1921).

Syn. *Tylenchus clavicaudatus* Micoletzky, 1921.

MORPHOLOGY. Dimensions :—1·23 mm.; $\alpha = 37$, $\beta = 10$, $\gamma = 9{\cdot}3$, V = 52·5%, stylet 6% œsophageal length. Only one female specimen seen; male unknown. Cuticle with fine transverse striæ, from 0·8μ to 1·2μ apart. The tail carries wider striæ 2·5-4μ apart. Lateral fields one-seventh to one-eighth diameter of body. Head not offset, without papillæ or radial ridges, rounded anteriorly. Stylet delicate and with weak basal swellings. Œsophagus and intestine typical. Rectum longer than anal body diameter. Gonads, paired, opposed and symmetrical, ovary clearly separated from uterus. Tail tapering sharply and uniformly to tip which is swollen to a rounded knob.

84

Fig. 84. *Anguillulina clavicaudata*. Female tail. (After Micoletzky.) No other drawings available.

OCCURRENCE. Very rare in heath pasture. Bukowina, Czernowitz, Rumania.

RELATIONSHIPS. Obscure. Micoletzky placed it near *T. granulosus* Cobb, but since this was described from immature forms and is a very vague species we are not helped much in attempting to classify Micoletzky's species. The knobbed tail is a distinctive feature.

REFERENCE. 84.

ANGUILLULINA GRACILOIDES Micoletzky, 1925.

Syn. *Tylenchus graciloides* Micoletzky, 1925.

MORPHOLOGY. Dimensions :—Two females only seen ; male unknown. Length, 1·5 mm. and 1·7 mm. ; $\alpha = 59$ and 60, $\beta = 8 \cdot 25$ and $8 \cdot 7$, $\gamma = 9$ and 10·3, V = 58% and 60%, anterior extent of ovary 20·3% and 28%, stylet 24μ or 13·2% of œsophagus and 28μ or 14% of œsophagus.

Body very slender. Cuticle with fine transverse striæ, latter about 1·2μ apart at middle of body. Lateral fields very delicate, not definitely seen. Head dome-like, lightly offset by constriction, cuticular ridges apparently absent. Stylet delicate, long and clearly knobbed at base, anterior part more refractive than posterior part. Œsophagus typical, outlet from dorsal œsophageal gland by short duct just behind base of stylet. Intestine normal ; anus indistinct.

Gonad anterior, no post-vulval uterine sac present. A receptaculum seminis seen between uterus and ovary. No eggs seen. Tail long, tapering gradually to the tip.

OCCURRENCE. From a shore meadow with Carex, Tjustrupsee, Denmark.

RELATIONSHIPS. Not closely related to any previously described species being distinguished by the long delicate stylet, slender body, the rather forwardly placed vulva without post-vulval sac and the long tapering tail.

REFERENCE. 86.

ANGUILLULINA EURYCEPHALA (de Man, 1921).

Syn. *Tylenchus eurycephalus* de Man, 1921.

MORPHOLOGY. Dimensions :—Described from one male specimen ; female unknown. Length, 0·72 mm. ; $\alpha = 110$, $\beta = 6$, $\gamma = 4 \cdot 5$.

Body extremely slender. Head with a lamellate dilatation of cuticle on each side extending about halfway down the head and making the latter as broad as long. de Man was uncertain whether the dilated cuticle extended all round the head or was confined to the true lateral regions. Buccal tube as long as head. Stylet weak and small but with distinct basal thickenings. Exact length not measured but from anterior end to base of stylet was 10μ, *i.e.*, about one-thirteenth of the œsophagus. Median bulb of latter not seen.

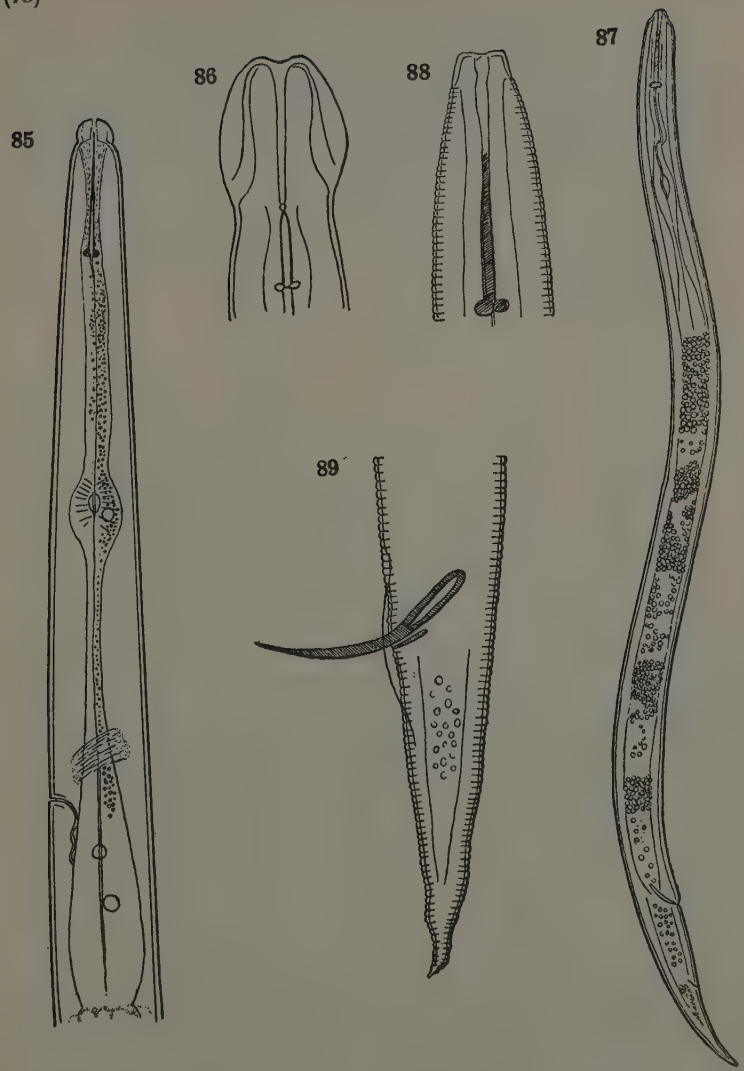


Fig. 85. *Anguillulina graciloides.* Œsophageal region, lateral view, × 765. (After Micoletzky.)

Fig. 86. *Anguillulina eurycephala.* Head end, × 3600. (After de Man.)

Figs. 87, 88 and 89. *Anguillulina macrophalla.* Adult female, × 500 ; head end and male tail more highly magnified. (After de Man.)

Bursa relatively small, 19μ long, *i.e.*, one-eighth the length of the tail. Spicules 9·6μ on the line drawn between the point and the head, simple in form, slightly arcuate, points very sharp. Tail a little more than one-third the distance between the end of the œsophagus and the anus, tapering gradually but not ending in a filiform process. Transverse striations of the cuticle were not seen.

OCCURRENCE. A slow moving species from sandy soil covered with herbage at the foot of dunes, Isle of Walcheren, Holland.

RELATIONSHIPS. None indicated.

REFERENCE. 81.

ANGUILLULINA MACROPHALLA (de Man, 1880).

Syn. *Tylenchus macrophallus* de Man, 1880.

MORPHOLOGY. Dimensions :—*Female* : length, 0·37 mm. ; $a = 25$–23, $\beta = 3{\cdot}75$–$3{\cdot}5$, $\gamma = 13{\cdot}5$–$12{\cdot}5$, V = 83%. *Male* : length, 0·33 mm. ; $a = 28$–27; $\beta = 3{\cdot}75$–$3{\cdot}5$, $\gamma = 11{\cdot}5$–$10{\cdot}5$.

de Man dealt with this species in his 1880 and 1884 papers, figuring it in the latter. Body tapering but very little anteriorly and considerably posteriorly to a narrow pointed tail. Cuticle with fine transverse striations. Head not offset, shaped like a truncated cone, no surface ridges. Stylet stout and large, being one-quarter the length of the œsophagus in the females and one-fifth in males. Œsophagus typical, median bulb larger in female than male, posterior region expanded.

FEMALE. Vulva placed very far posteriorly, gonad single, outstretched anteriorly.

MALE. Caudal wings very short, only extending a little in front and behind anus. Spicules comparatively large, long and narrow, slightly bent, points very sharp. Gubernaculum simple and very short.

OCCURRENCE. A remarkably small and active species from damp pasture soil in Holland.

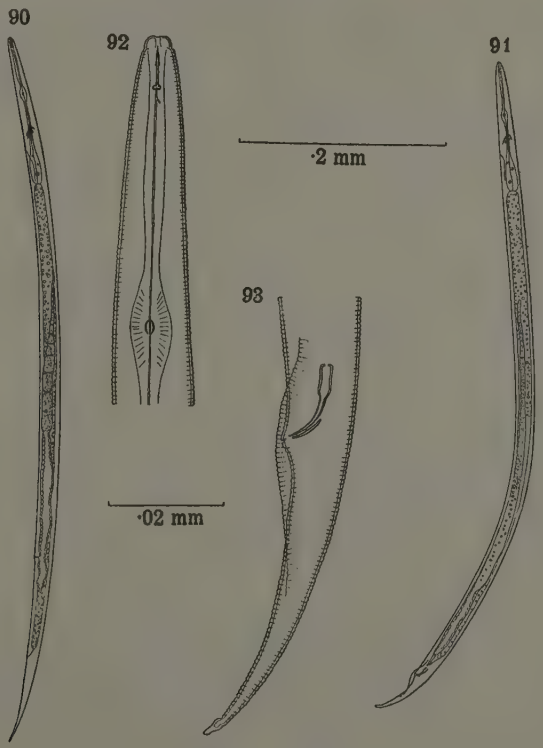
RELATIONSHIPS. Rather isolated and not clearly related to any other species.

REFERENCES. 76, 78, 94.

ANGUILLULINA INTERMEDIA (de Man, 1880).

Syn. *Tylenchus intermedius* de Man, 1880.

MORPHOLOGY. Dimensions :—*Female :* length, 0·56 mm. to 1·10 mm.; $a = 60–44$, $\beta = 9·5–5·5$, $\gamma = 10–8$, V = 68·5%–82·5%. *Male :* length, 0·65 mm. to 1 mm. ; $a = 60–40$, $\beta = 6·5–5$, $\gamma = 12·5–10$; spicules, 0·016 mm. ; stylet, 7·5μ–8μ in both sexes.



Anguillulina intermedia.

Figs. 90 and 91. Adult female and male, respectively. Upper scale.
Figs. 92 and 93. Anterior end and male tail, highly magnified.

A species of very variable length, but generally very slender. Body tapering a little anteriorly and considerably posteriorly to a pointed tail,

which, however, is not hair-like. Head offset by slight constriction, convex conical in shape, showing six radial surface ridges. Stylet very small and delicate, but of usual structure, basal swellings distinct. Œsophagus typical, median bulb rather elongate, anterior and neck regions narrow. Intestine, rectum, anus, nerve ring and excretory pore typical.

FEMALE. Vulva at about the beginning of the posterior third or quarter of body, gonad anterior ; a post-vulval uterine sac present.

MALE. Caudal alæ narrow, arising a little in front of heads of spicules and inserted about midway between anus and tip of tail. Spicules pointed and expanded anteriorly almost as in *A. dipsaci*. Gubernaculum simple, about one-third length of spicules.

OCCURRENCE. Widespread in soils of various types around the roots of plants. de Man remarked on its active motility.

RELATIONSHIPS. Rather closely related to *A. dipsaci* in general structure, but differing from that species in its smaller size, smaller stylet, in the more forwardly placed vulva and in the shorter caudal alæ.

REFERENCES. 60, 76, 78, 84, 86.

ANGUILLULINA BACILLIFER (Micoletzky, 1921).

Syn. *Tylenchus bacillifer* Micoletzky, 1921.

A species based on the study of three females, two of which were immature forms; males unknown.

MORPHOLOGY. Dimensions :—Length, 0·88 mm. ; $a = 38·3$, $\beta = 6·8$, $\gamma = 14·6$, V = 87%, anterior ovary, 52·5%, stylet, 18% œsophagus length.

Body slender. Cuticle with fine transverse striations about $1·1\mu$ wide. Lateral fields one-fourth to one-fifth width of body. Head not offset, convex conical in shape with rounded anterior face. No papillæ or radial surface ridges, but apparently three short comma-shaped cuticular rods, serving possibly as stylet guides, and occupying the situation usually taken by the buccal tube. Stylet small and delicate, posterior end only faintly thickened. Œsophagus, intestine, nerve ring and excretory pore normal. Vulva rather posteriorly placed, distance between vulva and anus equal to length of tail. No post-vulval uterine sac present. Tail conical, tapering to fairly sharp but rounded point.

OCCURRENCE. Very rare, from alpine pasture, Steiermark, Austria.

RELATIONSHIPS. Micoletzky at first took this for a variety of *A. dipsaci*. From this species, however, it is clearly distinguished by the structure of the head and by the absence of a post-vulval uterine sac.

REFERENCE. 84.

ANGUILLULINA BREVICAUDA (Micoletzky, 1925).

Syn. *Tylenchus brevicauda* Micoletzky, 1925.

This species is based on the study of two females and one male.

MORPHOLOGY. Dimensions : — *Female :* length, 0·46 mm. and 0·535 mm. ; $a = 37$ and 38, $\beta = 5·3$, $\gamma = 11·1$ and 13·8, V = 81% and 78% ; stylet, 8·5μ and 6·7μ respectively. *Male :* length, 0·43 mm. ; $a = 39$, $\beta = 6·1$, $\gamma = 10$; stylet, 8μ ; spicules, 11·8μ on the line from head to point.

Body slender, cuticle with fine transverse striations about 0·6–0·8μ wide. Lateral fields a little less than one-fourth body width. Head in the form of a rounded cap, rather refractive in appearance, not offset by constriction and apparently without surface ridges. Stylet moderately stout, but delicate in appearance, basal swellings not very distinct. Œsophagus, nerve ring and excretory pore typical. Intestine with large vacuoles or granules, possibly fat bodies, reaching 3·3μ in diameter.

FEMALE. Ovary directed forwards. Rather wide at its anterior end, a short post-vulval uterine sac present slightly shorter than the body is wide at the vulva.

MALE. Spicules rather short, points sharp, head rather expanded. Caudal alæ very small, arising at about the level of heads of spicules and inserted at about the anterior third of the tail, edge crenate. Tail in both sexes tapering gradually to a sharp tip.

OCCURRENCE. Found in an aquarium with " Krustensteine " from Tjustrupsee, Denmark.

RELATIONSHIPS. Placed by Micoletzky close to *A. bacillifer* and *A. paragracilis*. Differing from the former in having a stylet with basal thickenings and a more forwardly placed vulva and from the latter in the absence of radial head ridges and in the shape of the stylet. Differing from *A. filiformis* in its shorter tail and in the shape of the head.

REFERENCE. 86.

ANGUILLULINA MEDITERRANEA (Micoletzky, 1922).

Syn. *Tylenchus mediterraneus* Micoletzky, 1922.

MORPHOLOGY. Dimensions :—*Female :* length, 0·81 mm.; $a = 40$, $\beta = 7{\cdot}8$, $\gamma = 10{\cdot}6$, V = 69·5%. *Male :* length, 0·56 mm. to 1·1 mm. Micoletzky indicates chiefly its different dimensions from those of *A. fucicola*, to which he considered it very closely related. Stylet 17μ to 17·6μ long or one-ninth to one-seventh the œsophageal length as compared with one-thirteenth to one-fifteenth this length in the case of *A. fucicola*. The caudal alæ do not extend so far posteriorly in *A. mediterranea*, as in *A. fucicola*. The gubernaculum is smaller and has a wavy outline in the new species, whereas it is longer and is straight in *A. fucicola*. The tip of the tail, as figured by Micoletzky, has a small ventral hook as in *A. fucicola*.

OCCURRENCE. Free-living amonsgt algæ on the coasts of Mediterranean, Red Sea and Sea of Marmora.

RELATIONSHIPS. Micoletzky looked upon it as the free-living stem form from which the parasitic species *A. fucicola* may have arisen.

REFERENCE. 85.

ANGUILLULINA AGRICOLA (de Man, 1884).

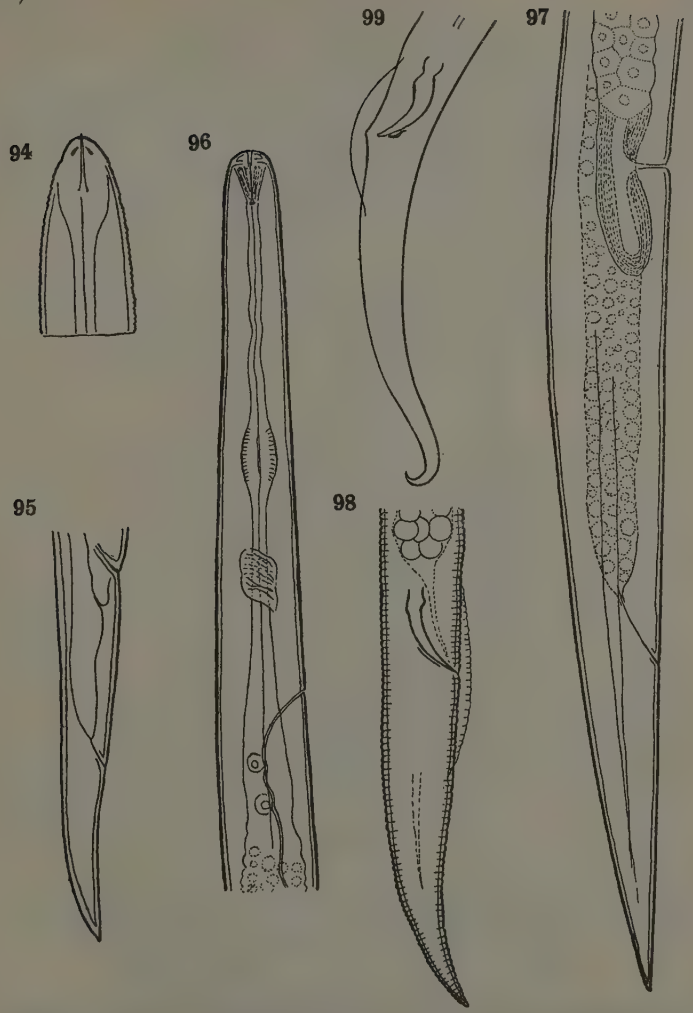
Syn. *Tylenchus agricola* de Man, 1884.
Tylenchus filiformis de Man, 1880.

Nec. *Tylenchus filiformis* v. Linst., 1876.

MORPHOLOGY. Dimensions :—*Female :* length, 0·6 mm.; $a = 30$–25, $\beta = 6$–5, $\gamma = 4{\cdot}3$, V = 60%. *Male :* length, 0·6 mm.; $a = 33$–28, $\beta = 6$–5, $\gamma = 3{\cdot}25$–$3{\cdot}0$.

Body tapering a little anteriorly and considerably posteriorly to a filiform tail. Cuticle with rather coarse transverse striæ which are also present on the head. Latter slightly offset, shaped like a truncated cone, apparently without surface ridges. Stylet well developed, typical in shape and with distinct basal swellings, about one-seventh the total distance from anterior end to beginning of intestine. Œsophagus, intestine, nerve ring and excretory pore typical.

FEMALE. Vulva leading to short vagina with thickened convex walls.



Figs. 94 and 95. *Anguillulina bacillifer*. Head and tail of female. (After Micoletzky.)

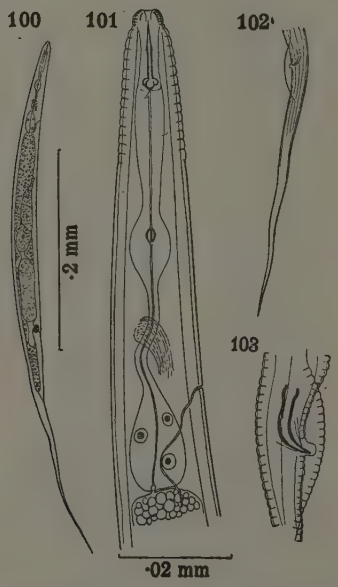
Figs. 96, 97 and 98. *Anguillulina brevicauda*. Œsophageal region, female tail and male tail, respectively, × 1500. (After Micoletzky.)

Fig. 99. *Anguillulina mediterranea*. Male tail, lateral view, × 850. (After Micoletzky.)

Gonad anterior, a short post-vulval uterine sac present. Tail long and whip-like.

MALE. Caudal alæ short, extending but very little in front and behind anus. Spicules moderately narrow, slightly arcuate, points sharp, heads expanded somewhat. Gubernaculum absent.

OCCURRENCE. A species of frequent occurrence in most types of soil.



Figs. 100-103. *Anguillulina agricola.* Fig. 100, female under low power; fig. 101, head and œsophagus highly magnified (original); figs. 102 and 103, male tail; fig. 103, caudal ala and spicule, highly magnified. (After de Man.)

RELATIONSHIPS. Closely related to *A. filiformis*, *A. bryophila*, *A. costata* and *A. leptosoma*, all species with long filiform tails. Distinguished from these by presence of striations on head, large stylet and absence of gubernaculum.

REFERENCES. 78, 84, 86.

ANGUILLULINA BRYOPHILA (Steiner, 1914).
Syn. *Tylenchus bryophilus* Steiner, 1914.

Described by Steiner from females only.

MORPHOLOGY. Dimensions :—Steiner gave the following—length, 0·288 mm. to 0·522 mm. ; width, 0·014 mm. to 0·022 mm. ; œsophagus, 0·07 mm. to 0·13 mm. ; tail, 0·05 mm. to 0·1 mm. ; $\alpha = 21$–19, $\beta = 5$–4, $\gamma = 5$–$4{\cdot}7$, V = 60%.

Micoletzky (1921 and 1925) described forms which he classified as *bryophilus*, a variety of *T. agricola*. His dimensions are as follows, both sexes being described :—*Female :* length, 0·268 mm. to 0·54 mm.; $\alpha = 31{\cdot}6$–$19{\cdot}3$, $\beta = 7$–4, $\gamma = 6{\cdot}9$–3, V = 52%–72·5% ; stylet, 9·7μ to 12μ. *Male :* length, 0·35 mm. to 0.6 mm. ; $\alpha = 33$–30, $\beta = 6{\cdot}5$–$4{\cdot}9$, $\gamma = 4{\cdot}7$–$3{\cdot}3$.

Body tapering slightly anteriorly and considerably towards the tail, which is long and finely pointed. Cuticle coarsely striated. Lateral fields very clear. Head not offset, shaped like a truncate cone, without lips. Stylet typical and with distinct basal knobs. Gonad outstretched anteriorly, a short post-vulval sac present. Micoletzky gave very few details as to the males, merely saying that they are completely typical and lack a gubernaculum.

OCCURRENCE. Steiner's material came from soil beneath a cushion of moss. Micoletzky (1921) obtained examples fairly frequently from soil in pastures, woods, bogs and under moss. The material treated in his 1925 paper was from Carex and Sphagnum moors.

RELATIONSHIPS. Very closely akin to *A. agricola* but having a smaller stylet and no striations on head.

REFERENCES. 84, 86, 109.

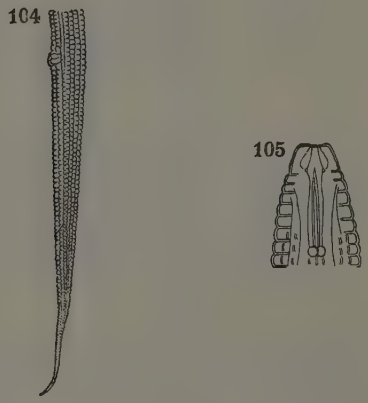
ANGUILLULINA COSTATA (de Man, 1921).
Syn. *Tylenchus costatus* de Man, 1921.

Described from two females only; male unknown.

MORPHOLOGY. Dimensions :—Length, 0·5 mm. and 0·516 mm. ; $\alpha = 30$–26, $\beta = 4{\cdot}7$, $\gamma = 6$, V = 66% ; stylet, 13·8μ.

Cuticle with coarse transverse striæ borne on 18 to 20 longitudinal ridges. Head almost hemispherical and laterally flattened, without

lips or papillæ. Stylet large with distinct basal swellings as in *A. agricola*, one-eighth œsophagus length. Latter also as in *A. agricola*, median bulb 14·4μ long, posterior swelling 21μ long by 10μ wide. Excretory pore 0·084 mm. from anterior end. Gonad single, directed forwards. Tail about equal in length to distance between vulva and anus, whereas in *A. agricola* the tail is about twice this length. de Man does not mention whether a post-vulval sac is present.



Figs. 104 and 105. *Anguillulina costata*. Fig. 104, posterior region of female, × 300; fig. 105, head of female, × 1200. (After de Man.)

OCCURRENCE. In moist soil covered with grass by the edge of river Mark, a small tributary of the river Breda, Holland.

RELATIONSHIPS. Closely resembling *A. cancellata* (Cobb) which may be identical with it. The present species, however, seems to have no striations on the head whereas these are found on *A. cancellata*. There are the same number of longitudinal ridges in each species and the vulva has practically the same relative position. Also closely akin to *A. agricola*.

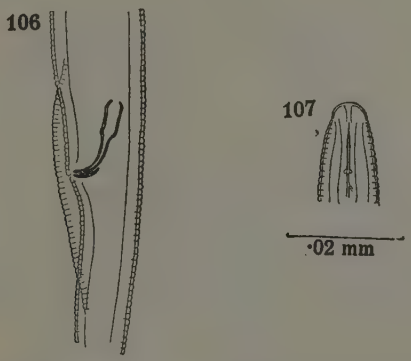
REFERENCE. 81.

ANGUILLULINA FILIFORMIS (Bütschli, 1873).

Syn. *Tylenchus filiformis* Bütschli, 1873.
Tylenchus elegans de Man, 1876.
Tylenchus exiguus de Man, 1876.
Tylenchus pillulifer v. Linstow, 1877.

Nec. *Tylenchus filiformis* de Man, 1876.

MORPHOLOGY. Dimensions :—*Female* : length, 0·45 mm. to 1·26 mm.; $a = 44–27, \beta = 7–4, \gamma = 8–4$, V = 61%–68%. *Male* : length, 0·54 mm. to 1·06 mm. ; $a = 55–27$, $\beta = 7–4$, $\gamma = 8–3$, ; stylet one-twelfth to one-fourteenth œsophagus length.



Figs. 106 and 107. *Anguillulina filiformis*. Head end and male tail, respectively, highly magnified. (Original.)

Body rather narrow, tapering anteriorly a little and posteriorly to a very fine whip-like tail. Cuticle with very fine transverse striæ, lateral fields moderately broad. Head scarcely offset, rather low and conical with rounded anterior face, no distinct lips or cuticular ridges. Stylet very delicate, scarcely knobbed basally. Rest of anatomy typical.

FEMALE. Gonad anterior, uterus with short post-vulval sac.

MALE. Caudal alæ short only reaching a little in front and behind anus. Spicules slightly arcuate, expanded at heads, points sharp. Gubernaculum present, about one-third length of spicules.

OCCURRENCE. A rather active species frequent in most kinds of soil around the roots of plants and amongst mosses, Carex and Sphagnum.

RELATIONSHIPS. de Man (1884) gave his own species, *exiguus* and *elegans* as synonyms of this species. Micoletzky (1921) also brought in *pillulifer* of v. Linstow. Very variable in size and differentiated from *A. agricola* by the more finely striated cuticle, the smaller stylet and the presence of a gubernaculum in the male.

REFERENCES. 10, 60, 73, 75, 78, 84, 86.

ANGUILLULINA LEPTOSOMA (de Man, 1880).

Syn. *Tylenchus leptosoma* de Man, 1880.

MORPHOLOGY. Dimensions :—*Female* and *male:* length, 0·66 mm.; $a = 55$–50, $\beta = 5{\cdot}66$–5, $\gamma = 3$, V = 55%–60%. Imamura (1931) gave *male*, 0·9 mm.; $a = 40{\cdot}9$, $\beta = 6$, $\gamma = 6$.

Body very slender, tapering slightly towards the head and considerably posteriorly to a long hair-like tail in both sexes. Cuticle with fine transverse striations only visible under high magnification. Head lightly offset, rounded in front and without lips or ridges. Stylet very small but knobbed basally and measuring about one-twelfth the distance from the head end to the beginning of the intestine. Œsophagus, intestine, nerve ring and excretory pore typical.

FEMALE. Vulva a little post-equatorial in position, vagina with thin walls, gonad anterior and with a short post-vulval sac.

MALE. Caudal alæ very short, extending but little in front and behind anus. Spicules very slender, points sharp, heads expanded a little. Gubernaculum absent.

OCCURRENCE. de Man spoke of it as a quick moving species of frequent occurrence in meadow and marsh soil.

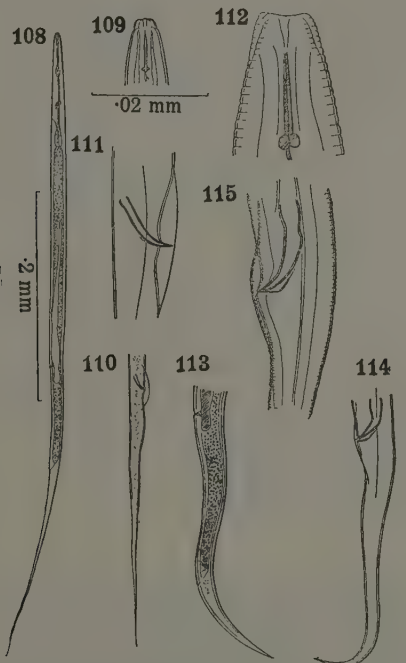
RELATIONSHIPS. Very closely related to *A. filiformis*, of which species Micoletzky (1921) classed it as a variety. It is, however, slenderer than that species and the male has no gubernaculum whereas one is present in *A. filiformis*. Differing from *A. agricola* in its finer striæ which are absent from the head but present on the head of *A. agricola* and in its smaller stylet.

REFERENCES. 60, 76, 78, 84.

ANGUILLULINA DAVAINII (Bastian, 1865).

Syn. *Tylenchus davainii* Bastian, 1865.

This was designated by Bastian type species of his genus Tylenchus in 1904.



Figs. 108-111. *Anguillulina leptosoma.* Fig. 108, young adult female, lateral view ; fig. 109, head highly magnified (original) ; fig. 110, male tail ; fig. 111, caudal alæ and spicules, highly magnified. (After de Man.)

Figs. 112-115. *Anguillulina davainii.* Fig. 112, head; fig. 113, female tail; fig. 114, male tail ; fig. 115, caudal alæ and spicules more highly magnified. (After de Man.).

MORPHOLOGY. Dimensions :—The following are combined from Micoletzky (1921) and (1925). *Female* : length, 0·65 mm. to 1·45 mm. ; $a = 38$–24, $\beta = 9{\cdot}3$–5, $\gamma = 9{\cdot}4$–$5{\cdot}6$, V = 54%–72% ; Stylet, 20μ. *Male* : length, 0·715 mm. to 1·13 mm. ; $a = 43$–$29{\cdot}7$, $\beta = 8{\cdot}5$–$5{\cdot}8$, $\gamma = 8{\cdot}5$–$5{\cdot}6$.

Body in both sexes tapering a little anteriorly and considerably behind to a long finely pointed tail of very variable length. Cuticle finely striated; striations also present on head; lateral fields rather broad. Head scarcely offset, shaped like a truncate cone and with the anterior face depressed. Stylet stout with prominent basal thickenings being about one-ninth as long as the œsophagus. Median bulb of œsophagus rather small. Other organs typical.

FEMALE. Gonad single, directed forwards, a short post-vulval sac present.

MALE. Caudal wings very short extending but a short distance in front and behind anus, edge crenate. Spicules sharply pointed, heads expanded. Gubernaculum more or less curved, about one-third the length of the spicules.

OCCURRENCE. Found originally in a sheet of moss covering a boulder in a freshwater stream at Falmouth. de Man found it in moist pasture and sandy dune soil. Micoletzky gives it principally as a moss dweller. It has been found by others around grass roots. Said to be very active.

RELATIONSHIPS. Fairly closely akin to *A. agricola* and *A. filiformis* but differing from the latter in having a large stylet and from the former in the male having a gubernaculum.

REFERENCES. **2, 78, 84, 86.**

ANGUILLULINA WEIDENBACHII (Rahm, 1924).

Syn. *Tylenchus weidenbachii* Rahm, 1924.

Description based of 62 sexually mature females and 16 males.

MORPHOLOGY. Dimensions :—*Female* : length, 0·585 mm. to 0·879 mm.; $a = 28–25$, $\beta = 7–6$, $\gamma = 8·5–6$, V = 70%–75%; eggs in uterus, 0·048 mm. by 0·023 mm. *Male:* length, 0·816 m. to 0·858 mm.; $a = 34–30$, $\beta = 8–6·5$, $\gamma = 9–6$.

Rahm considered this as possibly a local variety of *A. davainii* but differing in its smaller size, in a more strongly striated cuticle, in the vulva being more posteriorly situated and in the absence of a gubernaculum in the male. The tail and the spicules as in *A. davainii*.

OCCURRENCE. A more sluggish species than *A. davainii*. Sexually ripe forms found in September and October on Tortula.

REFERENCE. **94.**

ANGUILLULINA EMARGINATA (Cobb, 1893).

Syn. *Tylenchus emarginatus* Cobb, 1893.

MORPHOLOGY. Dimensions :—Cobb gives the following formulæ—

Female	3·3	10·	16·	—65·[45]	78·	0·68 mm.
	2·3	3·	3·5	3·2	2·	
Male	4·	12·	21·	—M	77·	0·6 mm.
	2·2	3·	3·4	3·5	3·	

Cuticle transversely striated. Neck conoid. Head about half as wide in front as at the level of the base of the stylet. Latter 20μ long, slender but with three distinct basal knobs. Œsophagus, intestine, nerve ring, excretory pore, rectum and anus typical.

FEMALE. Vulva about two-thirds body length from anterior end. Uterus with one or two eggs at a time. Eggs 0·056 mm. by 0·016 mm.

MALE. The caudal wings of the male are characterised by a re-entrant angle where they join the body post-anally. They extend an equal distance in front and behind the anus. No particulars given about spicules and gubernaculum.

OCCURRENCE. In soil from hills opposite Harwood, Clarence River, New South Wales, Australia.

RELATIONSHIPS. Obscure, but the form of the tail and the size of the stylet relate it to *A. davainii*.

REFERENCES. 15, 84.

ANGUILLULINA TERRICOLA (Bastian, 1865).

Syn. *Tylenchus terricola* Bastian, 1865.

MORPHOLOGY. Dimensions :—*Female:* length, 0·54 mm. ; width, 0·0203 mm. ; $\alpha = 26{\cdot}5$, $\beta = 6$, $\gamma = 16{\cdot}4$, V = 66%–68% ? ; stylet, 10μ. Male unknown.

Body tapering slightly forwards and considerably backwards to a pointed conical tail. Cuticle transversely striated. Stylet, œsophagus and intestine normal.

OCCURRENCE. From sandy soil adhering to wheat plant, Berkshire.

RELATIONSHIPS. Obscure. From its length, size of the stylet and shape of the tail, as well as the position of the vulva, it may be related to *A. filiformis*.

REFERENCE. 2.

ANGUILLULINA FARWICKI (Rahm, 1924).

Syn. *Tylenchus farwicki* Rahm, 1924.

Description based on five females; male unknown.

MORPHOLOGY. Dimensions :—Length, 0·4 mm. to 0·565 mm.; $a = 30–28$, $\beta = 4·8–4$, $\gamma = 15$, V = 66%.

Body rather slender, tapering somewhat anteriorly. Head scarcely offset and with rudimentary lips. Stylet of stout build, knobbed basally and about one-sixth as long as distance from head end to beginning of intestine. Median œsophageal bulb oval, posterior glandular part broad. Tail conical and tapering gradually to a sharp point. No eggs seen in uterus.

OCCURRENCE. On the liverwort, *Marchantia polymorpha* L, at Frullania, Prussian Rheinland.

RELATIONSHIPS. Rahm stated that it was closely related to *Tylenchus agricola* Bastian, presumably meaning *terricola* Bastian, but differing from that in the shape of the tail and the position of the vulva. It is clear from the dimensions that the vulva has practically the same relative position in both species; the tail, as figured by Rahm, certainly seems stouter than in Bastian's figure of *T. terricola*. Possibly the two species are identical, but so little detailed information is available concerning them that it is difficult to form an opinion. Perhaps they should both be relegated to species inquirendæ.

REFERENCE. 94.

ANGUILLULINA UNIFORMIS (Cobb, 1893).

Syn. *Tylenchus uniformis* Cobb, 1893.

The following formulæ are given by Cobb. No drawings given.

Female	1·8	?	?	—45·[45]	88·	0·63 mm.
	1·9	?	?	2·5	2·2	
Male	1·8	10·	18·	—M	90·	0·64 mm.
	1·2	2·5	2·8	2·7	1·8	

Striations of cuticle only visible under very high magnification. Head not offset by constriction. Stylet slender, one and a half times as long as width of head. Œsophagus, intestine, nerve-ring and excretory pore typical. Anus inconspicuous.

FEMALE. Vulva depressed, but easily visible; gonad anterior, a rudimentary post-vulval uterine sac present. Tail conical.

MALE. Caudal alæ inconspicuous, extending to the anterior fourth of the tail and an equal distance behind the anus. Spicules cuneiform, about 23μ long, pointed posteriorly and with expanded heads. Gubernaculum about one-fourth the length of the spicules. Testis anterior.

OCCURRENCE. In soil about the roots of sugar cane, at Harwood, Clarence River, New South Wales, Australia.

RELATIONSHIPS. A rather isolated species, but possibly related to *A. filiformis* as Micoletzky (1921, p. 551) suggests. The forward position of the vulva renders it rather difficult to place this species.

REFERENCES. 15, 84.

ANGUILLULINA MINUTA (Cobb, 1893).

Syn. *Tylenchus minutus* Cobb, 1893.

Cobb gives the following formula for the male; female unknown. No drawings given.

Male	2·7	14·	22·	M.	75·	0·4 mm.
	1·8	3·	3·	3·	2·4	

Striations on cuticle not found. Anterior third of neck region conoid. Head almost truncate. Stylet typical, about 10·8μ long. Œsophagus, intestine, nerve ring and excretory pore typical. Tail conical. Caudal alæ very small and inconspicuous, extending postanally for about three times the anal body-diameter and pre-anally about half as far. Spicules about 19·2μ long, pointed posteriorly and with the front ends not specially differentiated from the shaft. Guberbaculum about half as long as spicules, simple and closely parallel to spicules.

OCCURRENCE. Roots of sugar cane, Harwood, Clarence River, New South Wales, Australia.

RELATIONSHIPS. Obscure. The long conical tail relates it to *A. filiformis*, from which it is separated by the absence of striations on the cuticle.

REFERENCES. 15, 84.

ANGUILLULINA PARAGRACILIS (Micoletzky, 1921).

Syn. *Tylenchus* (*Chitinotylenchus*) *paragracilis* Micoletzky, 1921.

Description based on one female only; male unknown.

MORPHOLOGY. Dimensions:—Length, 0·7 mm.; $a = 32$, $\beta = 6{\cdot}4$, $\gamma = 11{\cdot}4$, V = 81%, anterior extent of ovary, 55·5%; stylet, one-thirteenth œsophageal length. Body rather slender, head end about one-third maximum breadth, diameter at anus about two-thirds same. Cuticle very delicate, transverse striæ only visible under oil-immersion. Head slightly offset, cuticular ridges on surface and forming a head

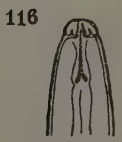


Fig. 116. *Anguillulina paragracilis*. Head end, only figure available. (After Micoletzky.)

Fig. 117. *Anguillulina annulata*. Head of female, × 814. (After Cassidy.)

framework uniting towards centre to form buccal tube. In optical section cuticular thickenings appearing as rods. Stylet moderately stout and cleft basally so that the three knob-like thickenings are widely separated, somewhat like an inverted Y. Œsophagus, intestine, nerve ring and excretory pore typical. Vulva prominent, slightly swollen with cuticularised edges. Gonad anterior, no post-vulval uterine sac. Tail short, plump, but rather sharply pointed at tip.

OCCURRENCE. Extremely rare, found in an alpine pasture, Steiermark, Austria.

RELATIONSHIPS. Separated from other species by the Y shaped stylet.

REFERENCE. 84.

ANGUILLULINA ANNULATA (Cassidy, 1930).

Syn. *Tylopharynx annulatus* Cassidy, 1930 (in litt).

Cassidy (1930) gave a brief description of a nematode under the name of *Tylopharynx annulatus* Cassidy (in litt.), as follows :—" A new species not hitherto recognised in Hawaii. This nematode is possessed of a strong, highly chitinized tripartite spear and was found very abundantly around the roots of sugar cane growing upon land previously in rice. In many ways it resembles the endoparasitic *Tylenchus similis*, but as yet this genus (*Tylopharynx*) has not been observed within the internal root structures of the cane."

MORPHOLOGY. Dimensions :—The only one given is that of an adult female as 0·65 mm. long. The following portions of the body are shown in a figure :—Head and œsophageal region, middle region of body including vulva and gonad, end of intestine to tip of tail, end view of head. From these drawings it can be seen that the cuticle is coarsely striated, that the tail tapers slightly to a blunt tip and that the stylet is shaped like an inverted Y with the knob-like swellings at the ends of the limbs. The œsophagus has a median muscular bulb and a posterior pyriform swelling as in Anguillulina species. The stylet is like that in *A. paragracilis*, and quite unlike the buccal apparatus found in the only known species of Tylopharynx, namely *T. striata*, the structure of which has been described in detail by the present writer (1929). There it is shown that it consists of three rods, one ventral and two dorso-lateral, the latter being stouter than the former and furnished towards their posterior ends with an outwardly projecting stalk on the end of which is an empty vescicle. The ventral rod has no lateral stalk. Anteriorly the two dorso-lateral rods abut on a complex horseshoe-shaped arrangement of articulating pieces. The whole structure bears no resemblance at all to the compact stylet of Anguillulina. Tylopharynx, in fact, is a genus which does not belong to the sub-family Anguillulininæ.

On account of the shape of the œsophagus and the resemblance of the stylet to that of *A. paragracilis* the writer has ventured to transfer the species from Tylopharynx to Anguillulina at any rate until such time as the full account of the male worm is published when a more trustworthy view of the systematic position can be formed.

REFERENCES. 12, 46a, 84.

SPECIES INQUIRENDÆ.

ANGUILLULINA GRANULOSA (Cobb, 1893).

Syn. *Tylenchus granulosus* Cobb, 1893.

Cobb gives the following formula for the female; male unknown. No drawings given.

Female	2·8	10·	16·	56·	90·	0·68 mm.
	2·3	2·7	2·8	3·3	2·4	

Cuticle with transverse striations. Neck conoid. Head rather rounded in front and with six somewhat spherical lips. Stylet stout with three basal swellings. Œsophagus, intestine, nerve ring and excretory pore typical. Only sexually immature specimens seen, consequently no information available as to position of vulva and gonads. Tail conoid to a blunt rounded terminus.

OCCURRENCE. Observed in numbers in brown rotten cavities in root-stock of banana plants, Fiji, also in outer sheaths of plants as well as in adjacent soil.

RELATIONSHIPS. Obscure, but from their size, the shape of the tail and the situation in which they were found, they may perhaps have been immature examples of *A. pratensis* or *A. musicola*.

REFERENCES. 14.

ANGUILLULINA MINIMA (Rahm, 1924).

Syn. *Tylenchus minimus* Rahm, 1924.

Description based on five immature females and three males.

MORPHOLOGY. Dimensions :—*Females* : length, 0·2 mm. to 0·372 mm.; $a = 18–17$, $\beta = 5–4·75$, $\gamma = 10·5–10$, V = 66%. *Males*: length, 0·5 mm. to 0·6 mm.; $a = 24–21$, $\beta = 5·5–5$, $\gamma = 24–20$; spicules, 18μ to 21μ.

Rahm placed these worms in the genus Tylenchus but expressed a doubt as to whether the males should really be reckoned as belonging to the genus since they lacked caudal alæ and showed three post-anal caudal papillæ. Head clearly offset but without any sign of lips. Stylet delicate but with basal thickenings, about one-fifth the length of the œsophagus. Latter with rather indistinct median bulb and an ovoid posterior swelling. Excretory pore not seen. One egg seen in uterus. Tail tapering to

conical point. Spicules in male narrow, an accessory piece present.

OCCURRENCE. On Tortula.

REFERENCE. 94.

ANGUILLULINA ORYZÆ (Breda de Haan, 1902).

Syn. *Tylenchus oryzæ* Breda de Haan, 1902.

MORPHOLOGY. Dimensions :—*Female* : length, 1·5 mm. to 1·82 mm. ; width, 0·042 mm. ; stylet, 19μ ; $a = 43$–25, $\beta = ?$, $\gamma = 19{\cdot}1$, V = 63·5% ; eggs, 102μ long by 26μ wide. No measurements given for males but said to be slightly smaller than females. Tails pointed and sometimes carrying a spine-like terminus. Male tail said to have caudal wings, a pair of spicules present. No details as to gonad in either sex but presumably only a single ovary, since it is referred to in the singular throughout.

OCCURRENCE. Roots of rice and considered to be the cause of a disease. Butler, however, in his paper (1913) on *A. angusta* mentions, in a footnote, that they are not the cause of the disease.

RELATIONSHIPS. Very obscure. Their considerable length renders it difficult to relate them to any of the free-living species found on the roots of plants except to *A. robusta* and *A. macrura*.

REFERENCE. 52.

ANGUILLULINA SACCHARI (Soltwedel, 1888).

Syn. *Tylenchus sacchari* Soltwedel, 1888.

The writer has been unable to consult Soltwedel's original paper as, so far as can be ascertained from an extensive search of libraries, etc., the journal in which it was published does not appear to be in this country. The same applies also to Krüger's paper (1890). The following dimensions are based on those given by Zimmermann (1898) in the paper in which he described his *Tylenchus coffeæ*.

MORPHOLOGY. Dimensions :—*Female* : length, 0·58 mm. to 0·77 mm. ; stylet, 12μ ; $a = 25{\cdot}6$, $\beta = ?$, $\gamma = 12{\cdot}9$, V = 80%. *Male* : length, 0·71 mm. ; $a = 28$, $\beta = ?$, $\gamma = 12{\cdot}9$. In the same table from which these are taken he gives measurements based on Krüger's paper as follows :—*Female* : length, 0·81 mm. ; $a = 23{\cdot}25$, $\beta = ?$, $\gamma = 20$, V = 86·5%. *Male* : length, 0·78 mm. ; $a = 32{\cdot}2$, $\beta = ?$, $\gamma = 12{\cdot}5$.

Tail short and blunt as in *A. pratensis*. The two points which Zimmermann emphasised in discussing the relationships of his *Tylenchus coffeæ* to *T. sacchari* were (1) the position of the excretory pore, which Soltwedel placed rather far forward on the body, at 27μ from the anterior end, as against 80μ for the same distance in *T. coffeæ*; and (2) the much larger eggs which Soltwedel gave as 0·1 mm. by 0·025 mm. as against 0·054 mm. by 0·025 mm. in the case of *T. coffeæ*. With regard to these two points it is sufficient to point out that variability in size of eggs has already been discussed in considering *A. pratensis*, where it is shown that great variations in size may be found. The forward position of excretory pore may perhaps be an error of observation or measurement since this structure is often very difficult to locate. Considering these points and the fact that Zimmermann himself recognised the close similarity of the worms to his *T. coffeæ*, the writer is inclined to regard *A. sacchari* as probably synonymous with *A. pratensis*, but in the absence of more detailed information on points of anatomy has considered it advisable to class it as a species inquirenda.

ANGUILLULINA TURBO (Marcinowski, 1909).

Syn. *Tylenchus turbo* Marcinowski, 1909.

Described from the larval stage only. Length, 0·39 mm.; œsophagus, 0·1 mm.; tail, 0·046 mm.; $a = 20$–19, $\beta = 3{\cdot}9$, $\gamma = 8{\cdot}48$. The worms occurred in numbers in rotting potatoes.

REFERENCE. 82.

ANGUILLULINA VELATA (Bütschli, 1873).

Syn. *Tylenchus velatus* Bütschli, 1873.

Only males seen; females unknown.

MORPHOLOGY. Dimensions:—Length, 0·88 mm.; width, 0·019 mm.; $a = 45$, $\beta = ?$, $\gamma = 25$. Stylet rather smaller than in *A. davainii*, *i.e.*, less than 20μ. Œsophagus very indistinct; the drawing given by Bütschli shows no median bulb or distinct posterior swelling. Possibly the specimen drawn may have been an old degenerate one. Caudal alæ large and broad, enclosing all but the tip of the tail. Spicules said to be rather narrower than those of *A. davainii* but of the same general shape.

OCCURRENCE. On the roots of a moss.

RELATIONSHIPS. Very obscure.

REFERENCE. 10.

Nomina Nuda.

TYLENCHUS BIOCULATUS Zimmermann, 1904. This is listed by Stiles and Hassall (1920), page 834. They indicate, however, that it was given by Embleton in the Zoological Record, Vol. XLI, for 1904, page 54, who ascribed it to Zimmermann. The paper by this author, however, contained no such name.

TYLENCHUS COBBI de Man, 1906. This name was proposed by de Man for *Tylenchus gracilis* Cobb, 1888. The latter was described by Cobb as a Tylenchus species from around the roots of grass. In his paper on Strawberry-bunch (1891), page 8, he transferred the species to Aphelenchus, making it *Aphelenchus gracilis*, a fact which appears to have escaped the notice of most systematists dealing with these genera subsequently. The name, *Tylenchus cobbi*, therefore lapses as a nomen nudum.

TYLENCHUS FALCARIÆ Oerley, 1880. v. Frauenfeld described the presence of nematode worms in galls on the leaves of Falcaria from the vicinity of Vienna in 1872 and called them Anguillulas without a specific name. Oerley proposed the name *T. falcariæ*. As, however, there is no description or definition of the worms the name becomes a nomen nudum.

TYLENCHUS FŒNARIUS Kühn. This name is mentioned by Marcinowski (1909), page 125-6, who cites Kühn as using it as the name of a species causing violet-coloured galls on grass leaves. There does not appear to be any description or definition of this species.

TYLENCHUS LEONTOPODII Oerley, 1880. A name proposed by Oerley for a species of *Anguillula* found by v. Frauenfeld in the leaves of *Leontopodium alpinum* (Edelweiss). In the absence of any description or definition the name lapses as a nomen nudum.

TYLENCHUS NIVALIS Kühn (1880 ?). Cited in this form by Marcinowski (1909), page 125. Apparently it was proposed as the name for the eelworm causing galls on Edelweiss by Kühn. There appears to be no description or definition of the worms.

TYLENCHUS PELLUCIDUS (Bastian, 1865) Butschli, 1876. This is given by Stiles and Hassall (1920), p. 836. On referring to Bütschli (1876), p. 235, one finds the name *Tylenchus pellucidus* Bastian, mentioned in connection with rapid amœboid movements of the yolk in segmenting eggs of the worm which are illustrated on his plate II, figs. 16-21. In the explanation of the figures the worms are cited under their correct name of *Trilobus pellucidus*, a species made by Bastian. It is clear that the name, *Tylenchus pellucidus*, given in the text is either an uncorrected *lapsus* made by Bütschli or a printer's error and consequently must be considered as a nomen nudum.

TYLENCHUS TILIÆ Oerley, 1880. Apparently based on the fact that Butschli (1873), page 36, mentions buds of a lime tree from the vicinity of Darmstadt in which a Dr. Noll found some nematodes belonging to this genus. As, however, there is no description or definition of them the name lapses as a nomen nudum.

Alphabetical List of *Tylenchus* Species with their Present Status.

T. acutocaudatus Zimmermann, 1898 syn. of *A. similis*.
T. agricola de Man, 1884 becomes *A. agricola* (de Man, 1884).
T. agrostidis Bastian, 1865 wrong name for *T. agrostis*.
T. agrostis (Steinbuch, 1799) syn. of *A. agrostis* (Steinbuch, 1799) Goodey, 1932.
T. alatus Cobb, 1930 syn. of *A. alata* (Cobb, 1930) Goodey, 1932.
T. allii Beijerinck, 1883 syn. of *A. dipsaci*.
T. angustus Butler, 1913 syn. of *A. angusta* (Butler, 1913) Goodey, 1932).
T. apapillatus Imamura, 1931 becomes *A. apapillata* (Imamura, 1931).
T. arboricolus Cobb, 1922 syn. of *A. arboricola* (Cobb, 1922) Goodey, 1932.
T. arenarius (Neal, 1889) Cobb, 1890 syn. of *Heterodera marioni* (Cornu 1879) Goodey, 1932.

T. askenasyi Bütschli, 1873 syn. of *A. dipsaci.*

T. bacillifer Micol., 1921 becomes *A. bacillifer* (Micol., 1921).

T. balsamophilus Thorne, 1926 syn. of *A. balsamophila* (Thorne, 1926) Goodey, 1932.

T. biformis Cobb, 1909 syn. of *A. similis.*

T. bioculatus Zimmermann, 1904 nomen nudum.

T. brachyurus Godfrey, 1929 syn. of *A. pratensis.*

T. brevicauda Micol., 1925 becomes *A. brevicauda* (Micol., 1925).

T. browni Kreis, 1929 syn. of *A. dubia* (Bütschli, 1873).

T. bryophilus Steiner, 1914 becomes *A. bryophila* (Steiner, 1914).

T. bulbosus Micol., 1915 syn. of *Pathoaphelenchus parietinus.*

T. cancellatus Cobb, 1925 syn. of *A. cancellata* (Cobb, 1925) Goodey, 1932.

T. clavicaudatus Micol., 1921 becomes *A. clavicaudata* (Micol., 1921).

T. cobbi de Man, 1906 nomen nudum.

T. consobrinus de Man, 1906 to Hexatylus Goodey, 1926.

T. costatus de Man, 1921 becomes *A. costata* (de Man, 1921).

T. cylindricaudatus Steiner, 1926 syn. of *Aphelenchus cylindricaudatus* (Steiner, 1926) Steiner, 1931.

T. darbouxi Cotte, 1912 syn. of *A. darbouxi* (Cotte, 1912) Goodey, 1932.

T. davainii Bastian, 1865 becomes *A. davainii* (Bastian, 1865).

T. dendrophilus Marcin., 1909 syn. of *A. dendrophila* (Marcin., 1909) Goodey, 1932.

T. devastatrix (Kühn, 1868) syn. of *A. dipsaci.*

T. dihystera Cobb, 1893 syn. of *A. robusta* (de Man, 1876).

T. dipsaci (Kühn, 1858) Bast., 1865 syn. of *A. dipsaci* (Kühn, 1858) Gerv. and v. Ben., 1859.

T. dubius Bütschli, 1873 becomes *A. dubia* (Bütschli, 1873).

T. durus Cobb, 1922 syn. of *A. dura* (Cobb, 1922) Goodey, 1932.

T. elegans de Man, 1876 syn. of *A. filiformis.*

T. emarginatus Cobb, 1893 becomes *A. emarginata* (Cobb, 1893).

T. erythrinæ Zimmermann, 1904 syn. of *A. multicincta.*

T. eurycephalus de Man, 1921 becomes *A. eurycephala* (de Man, 1921)

T. exiguus de Man, 1876 syn. of *A. filiformis.*

T. falcariæ Oerley, 1880 nomen nudum.

T. Farwicki Rahm, 1924 becomes *A. farwicki* (Rahm, 1924).

T. filiformis Bütschli, 1873 becomes *A. filiformis* (Bütschli, 1873).

T. fœnarius Kühn, 1880? nomen nudum.

T. fucicola de Man, 1892 syn. of *A. fucicola* (de Man, 1892) Goodey, 1932.

T. fungorum Bütschli, 1873 to Hexatylus Goodey, 1926.

T. gracilis de Man, 1880 becomes *A. gracilis* (de Man, 1880).

T. gracilis Cobb, 1888 syn. of *Aphelenchus gracilis* Cobb, 1891.

T. graciloides Micol., 1925 becomes *A. graciloides* (Micol., 1925).

T. graminis (Hardy, 1850) Marcin., 1909 syn. of *A. graminis* (Hardy, 1850) Goodey, 1932.

T. granulosus Cobb, 1893 becomes *A. granulosa* (Cobb, 1893) sp. inq.

T. havensteinii Kühn, 1881 syn. of *A. dipsaci.*

T. hordei Schøyen, 1885 syn. of *A. radicicola* (Greeff, 1872) Goodey, 1932.

T. hyacinthi Prillieux, 1881 syn. of *A. dipsaci.*

T. imperfectus Bütschli, 1876 syn. of *Iotonchium imperfectum* Cobb, 1920.

T. intermedius de Man, 1880 becomes *A. intermedia* (de Man, 1880).

T. lamelliferus de Man, 1880 becomes *A. lamellifera* (de Man, 1880).

T. leontopodii Oerley, 1880 nomen nudum.

T. leptosoma de Man, 1880 becomes *A. leptosoma* (de Man, 1880).

T. macrophallus de Man, 1880 becomes *A. macrophalla* (de Man, 1880).

T. mahogani Cobb, 1920 syn. of *A. mahogani* (Cobb, 1920) Goodey, 1932.

T. mediterraneus Micol., 1922 becomes *A. mediterranea* (Micol., 1922).

T. millefolii Löw, 1874 syn. of *A. millefolii* (Löw, 1874) Goodey, 1932.

T. minimus Rahm, 1924 becomes *A. minima* (Rahm, 1924) sp. inq.

T. minutus Cobb, 1893 becomes *A. minuta* (Cobb, 1893).

T. mirabilis Bütschli, 1873 syn. of *Tylencholaimus mirabilis* (Büt., 1873) de Man, 1884

T. multicinctus Cobb, 1893 becomes *A. multicincta* (Cobb, 1893).

T. musicola Cobb, 1919 syn. of *A. musicola* (Cobb, 1919) Goodey, 1932.

T. nivalis Kühn, 1880? nomen nudum.

T. obtusus Bastian, 1865 becomes *A. obtusa* (Bastian, 1865).

T. olaæ Cobb, 1906 syn. of *A. multicincta.*

T. oryzæ de Haan, 1902 becomes *A. oryzæ* (de Haan, 1902) sp. inq.

T. paragracilis Micol., 1921 becomes *A. paragracilis* (Micol., 1921).

T. pellucidus (Bast., 1865) Bütschli, 1876 nomen nudum.

T. penetrans Cobb, 1917 syn. of *A. pratensis.*

T. phalaridis (Steinbuch, 1799) syn. of *A. agrostis.*

T. phlei Horn, 1889 name proposed for *T. phalaridis.*

T. pillulifer v. Linst., 1877 syn. of *A. filiformis.*

T. pratensis de Man, 1880 syn. of *A. pratensis* (de Man, 1880) Goffart, 1929.

T. procerus Bally and Reydon, 1931 becomes *A. procera* (Bally and Reydon, 1931).

T. pseudorobustus Steiner, 1914 syn. of *A. multicincta.*

T. putrefaciens Kühn, 1879 ? syn. of *A. dipsaci.*

T. radicicola (Greeff, 1872) Oerley, 1880 syn. of *A. radicicola* (Grf. 1872) Goodey, 1932.

T. robustus de Man, 1876 becomes *A. robusta* (de Man, 1876).

T. sacchari Soltwedel, 1888 becomes *A. sacchari* (Soltwedel, 1888) sp. inq.

T. scandens (Schneider, 1866) syn. of *A. tritici.*

T. schachtii (Schmidt, 1871) Oerley, 1880 syn. of *Heterodera schachtii* Schmidt, 1871.

T. secalis (Nitschke, 1868) Oerley, 1880 syn. of *A. dipsaci.*

T. setiferus Cobb, 1893 syn. of *Eutylenchus setiferus* Cobb, 1913.

T. similis Cobb, 1893 syn. of *A. similis* (Cobb, 1893) Goodey, 1932.

T. spiralis Cassidy, 1930 (in litt.) syn. of *A. multicincta.*

T. sycobius Cotte, 1920 syn. of *A. sycobia* (Cotte, 1920) Goodey, 1932.

T. symmetricus Cobb, 1914 becomes *A. symmetrica* (Cobb, 1914).

T. tenuis Micol., 1921 becomes *A. tenuis* (Micol., 1921).

T. terricola Bast., 1865 becomes *A. terricola* (Bast., 1865).

T. tiliæ Oerley, 1880 nomen nudum.

T. tritici (Steinbuch, 1799) syn. of *A. tritici* (Steinbuch, 1799) Gerv. and v. Ben., 1859.

T. turbo Marcin., 1909 becomes *A. turbo* (Marcin., 1909) sp. inq.

T. uniformis Cobb, 1893 becomes *A. uniformis* (Cobb, 1893).

T. velatus Bütschli, 1873 becomes *A. velata* (Bütschli, 1873) sp., inq.

T. weidenbachii Rahm, 1924 becomes *A. weidenbachii* (Rahm, 1924).

SPECIES BELONGING TO GENERA OTHER THAN *TYLENCHUS* BROUGHT INTO *ANGUILLULINA* IN THIS PAPER.

A. annulata (Cassidy, 1930) from *Tylopharynx annulatus* Cassidy, 1930 (in. litt.).

A. macrura nom. nov. for *Aphelenchus dubius* Steiner, 1914.

SPECIES REMOVED TO GENERA OTHER THAN *ANGUILLULINA* IN THIS PAPER.

T. fungorum Bütschli, 1873 and *T. consobrinus* de Man, 1906 to *Hexatylus* Goodey, 1926 as *H. fungorum* (Bütschli, 1873) and *H. consobrinus* (de Man, 1906).

NOTE.

TYLENCHUS TUMEFACIENS Cobb, *fide* Lounsbury (1925). In referring to a nematode parasitic on the lawn grass known as "Bradley" (a species of *Cynodon*) Lounsbury stated that Dr. N. A. Cobb proposed to describe it under the name of *Tylenchus tumefaciens*. In response to a request for information as to whether a description of this species had been published, Dr. Cobb kindly informed the writer by letter, dated December 4th, 1931, that he proposes to publish an account of it at an early date. It gives rise to galls on the stem, leaves and inflorescence.

This note has been added for the sake of completeness and because the name, *Tylenchus tumefaciens*, has been in the literature since 1925. REFERENCE. 73a.

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Journal of Helminthology, Vol. x, *Nos.* 2-3, *June*, 1932, *pp.* 181-182.

Preliminary Note on the use of Root Excretions as a Method of Controlling the Nematode *Heterodera schachtii.*

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Some preliminary experiments on the effects of potato root excretions in stimulating the larvæ of *H. schachtii* to hatch and emerge from the cyst, and the neutralisation of this stimulating factor by the root excretions of mustard seedlings, have already been described. Since chemical treatment of infected soil as a means of controlling the eelworm has been the subject of investigation in Europe for the past fifty years without yielding any results of practical value, investigations into the reactions of the parasites to the root excretions of plants were undertaken in the hope that some result might be attained which would point to a solution of the eelworm problem on biological lines. The high degree of specialisation shown by the British potato-strain rendered it peculiary suitable for investigations of this character.

Of the two lines on which investigations have been pursued, the more botanical side, dealing with the reactions of the parasite to the root excretions of various plants, has already given results which may be of interest to other workers. A study of the literature dealing with the more polyphagous strains of the nematode yielded indications of the lines on which preliminary experiments might be conducted, and laboratory experiments on the stimulant effects of grass root excretions were carried out. Very diverse results were obtained from different grass species, but some were found to exert a stimulant action, giving results very similar to those previously obtained with potato root excretions. Attempts were made to produce infections on these species, but

although the grasses were grown for two years in heavily infected soil, no infections were found, and it was therefore concluded that a fairly high degree of immunity existed in these cases to the strain of eelworm specialised for potato.

A field experiment in the area from which the soil used in the above tests was obtained, was therefore begun in 1931. Two seventeen-acre fields, adjacent to one another and undergoing the same rotation, both of which had shown eelworm damage to the potato crop of the previous year, were selected for the experiment. One was sown with a grass mixture in a cover crop of cereal, the other was kept as a control and planted with cereal only. Soil samples were taken in early spring from both fields before the grasses were sown, and again after the grain harvest. Cyst counts were made from measured soil samples and the relative numbers of unhatched eggs in fifty cysts from each sample were estimated by dissections and counts. The second samples were taken in September. It was then found that while in the control field the reduction in the number of cysts containing the full complement of unhatched eggs was negligible, the experimental field showed a reduction of 23·6 per cent. in the number of full cysts as compared with the January estimations, while the relative number of three-quarter-full, half-full and quarter-full cysts showed a corresponding increase. It is of interest to note that these differences not only occurred in the final averages but showed remarkable consistency throughout the individual samples.

This experiment is being continued and a full account of the second year's results will be published in due course. Meanwhile further laboratory studies on the effects of root excretions are in progress.

Preliminary investigations into the chemical side of the problem, the determination of the chemical composition of the stimulant substance in potato root excretions, have shown that the substance is non-volatile and can withstand drying without loss of efficiency.

Journal of Helminthology, Vol. x, No. 4, September, 1932, pp. 183-194.

On Three Species of the Genus *Capillaria* from the English Domestic Fowl.

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Introduction.

Owing to the lack of adequate descriptions and figures, the majority of the members of the Genus *Capillaria* are extremely difficult to identify. This is no doubt due, to some extent, to the fact that the worms are so slender that certain morphological features upon which species can be separated are difficult to observe without a very close examination of the worms under high magnification.

A study of these forms is also complicated by the fact that several members of the genus are often found in the same host and there is, therefore, no clue as to the identity of many of the species recorded by some of the earliest workers in this field. Added to this difficulty is the fact that the same species may be encountered in several hosts.

In no group is our knowledge so incomplete as in the case of the Capillarids of domestic birds although the forms in these hosts have been frequently met with and have often been referred to as the cause of considerable damage.

In this paper an account is given of studies made on some members of the Genus *Capillaria* found in domestic fowls. Three species in particular are described and figured and points of difference between them

are indicated. The other species recorded from this host are not described as the writer was unable to obtain specimens for study but certain features which distinguish them from the three species described below are referred to.

With regard to the question of synonymy the writer has not attempted to include a complete list for each species. The difficulties already referred to in connection with the identification of species makes it almost impossible, in the present stage of our knowledge, to come to any conclusion in the majority of instances and little would be gained by merely repeating the lists given by previous workers.

Source of Material.

The worms which are described in this paper were obtained from the small intestine and cæca of domestic fowls supplied by poultry farmers and dealers in the vicinity of the Institute of Agricultural Parasitology near St. Albans, Hertfordshire. In all, some 53 intestines from these birds were examined at different times during the last two years and, apart from noting the occurrence of some of the other types of worms met with, attention was chiefly paid to the members of the Genus *Capillaria*. The latter were found very frequently and in 42 of the fowls, where the intestine was examined separately, 17 were found to harbour one or more of the three species described below. By far the most common were *Capillaria longicollis* and *Capillaria columbæ* while *Capillaria retusa* was only found with certainty on three occasions. This latter figure is, however, probably too low since, in many of the birds examined, the cæcal contents were not separated from those of the small intestine and in the early stages of the work the differences between the species, particularly in the case of the female worms, were not fully appreciated.

It is not known whether *Capillaria annulata* does occur in this locality since it was only on a few occasions that the crop and the œsophagus could be obtained for examination and these shewed no trace of this parasite.

Description of Species.

CAPILLARIA LONGICOLLIS (Rud., 1819) Travassos, 1915.

Synonyms *Trichosoma longicolle* Rud., 1819.
Calodium caudinflatum Molin, 1858.
Trichosoma gallinum Kowal., 1894.
Trichosoma caudinflatum Kowal., 1901.

Following general usage the specific name *longicollis* is retained for the species described below although it is recognised that Rudolphi's brief description does not enable one to place his species with any degree of certainty. *Calodium caudinflatum* is included here as a synonym since Molin's figures for this species shew the presence of caudal alæ in the male and *C. longicollis* appears to be the only species in the fowl which shews this feature. On the other hand, Molin found his species in *Perdix coturnix* and further study may shew that the two forms are not identical. *Trichosoma gallinum*, which was described by Kowalewski (1894) from the fowl and later (1901) made a synonym of *T. caudinflatum* by the same author, is undoubtedly the same as the species described under the name *C. longicollis* in this paper.

In *C. longicollis* the body is long and slender and tapers gradually towards the head which ends bluntly. The greatest width is found in the posterior half of the body. There is a broad, lateral bacillary band present which extends along the whole length of the body ; a very narrow ventral band is also present. Two oval glandular bodies can easily be seen at the junction of the œsophagus and the intestine. The transverse striations which are present are very faint and can only be seen under high magnification.

Female.—The length of the female is from 14 mm. to 25·25 mm. with a maximum width of 0·07 mm. The width at the head end is slightly less than 0·01 mm. but reaches 0·055 mm. at the base of the œsophagus. After reaching its maximum width in the posterior half, the body narrows again towards the tail end which has a width of 0·042 mm. at the anus.

The region from the anterior end to the base of the œsophagus varies in length from 5 mm. to 7 mm. and is about one-third of the total length of the worm. There is a slight narrowing of the body between the

posterior end of the œsophagus and the slightly raised prominence behind this upon which the vulva is situated. The distance between the œsophagus and the vulva is from 0·1 mm. to 0·15 mm. A membranous appendage projecting outward from the vulva to a length of about 0·075 mm. is a conspicuous feature in this species and appears to be always present.

The tail end is characteristic in being cylindrical with almost parallel sides for a short distance in front of the anus. This feature serves to distinguish between the females of this species and those of the other two species described below.

The tip of the tail is bluntly rounded and the anus is sub-terminal. There is no indication of an inflation as shewn in the tail end of the female of *C. longicollis* recorded by Shipley (1909) from *Lagopus scoticus*.

The lateral bacillary bands have a width which is about one-third that of the body. There is, however, a good deal of variation in this relative width which depends to some extent on the point at which the measurement is made.

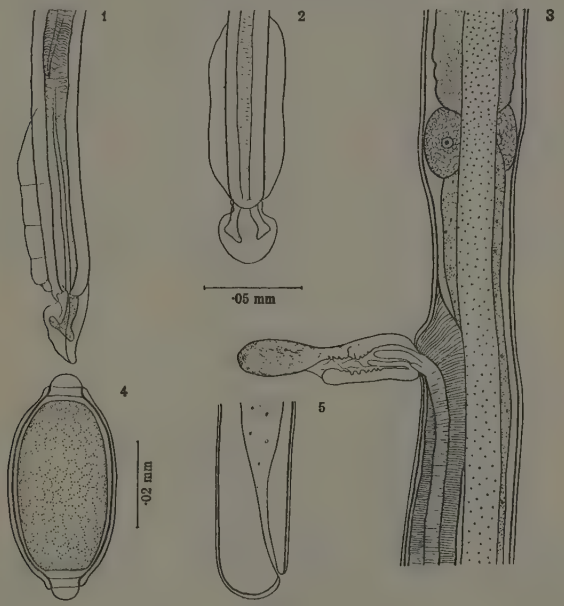
The eggs have an average measurement of 0·053 mm. in length by 0·023 mm. in width.

Male.—The male has a length varying from 9 mm. to 14 mm. and measures 4·5 mm. to 6·25 mm. from the head to the posterior end of the œsophagus. This region is, therefore, slightly less than half the total length of the body. The width is 0·007 mm. at the head end; 0·04 mm. at the base of the œsophagus; 0·03 mm. at the level of the anterior end of the spicule and 0·021 mm. in the region of the cloaca.

The spicule is very slender and has a length of 0·82 mm. to 1·07 mm. with a maximum width of 0·005 mm. The anterior end is not swollen as in the other species described below and the tip appears to be finely pointed. The posterior end of the spicule is, however, difficult to make out very clearly and in several of the specimens examined the end was slightly reflexed and thus gave the appearance of a blunt tip when viewed in certain aspects. The spicular sheath is smooth and shews transverse wavy markings in places.

The tail end of the male terminates in a broad heart-shaped bursa-like membrane which is supported by two processes; these processes are

somewhat T-shaped. There are two lateral caudal alæ present which emerge at about 0·1 mm. in front of the cloaca. The ventral margin of the cloaca projects slightly and thus gives the appearance of a short spine when the tail end is viewed laterally.



C. longicollis.

Fig. 1. Tail end of male, lateral view.
Fig. 2. Tail end of male, dorsal view.
Fig. 3. Region of vulva, lateral view.
Fig. 4. Egg under high magnification.
Fig. 5. Tail end of female, lateral view.
The lower scale refers only to Fig. 4.

The measurements given above for *C. longicollis* are considerably less in some respects than those given by other workers. It would appear that a good deal of variation, particularly in regard to length, does occur in this species since the length of the female as given by different authors shews a range extending from 25 mm. to 80 mm. It must be

noted however that this range covers the length of the representatives of this species found in a number of different hosts. These hosts include *Gallus domesticus*, *Phasianus colchicus*, *Chrysolophus pictus*, *Perdix perdix*, *Coturnix coturnix*, *Lyrurus tetrix*, *Tetrao urogallus*, and *Lagopus scoticus*, and the great variation in the length of the worm may be due either to host influence or to the existence of more than one species among the worms now included under the name *C. longicollis*. Furthermore, it would appear that the very small length given in this paper for this species is due to the fact that the worms examined were comparatively young adults and that a good deal of growth occurs, particularly in the region behind the vulva, after maturity is reached. This view is supported by the fact that the difference between the length of the region from the head to the posterior end of the œsophagus and that of the remainder of the worm tends to be greatest in the longest specimens.

CAPILLARIA COLUMBÆ (Rud.,1819) Travassos,1915.

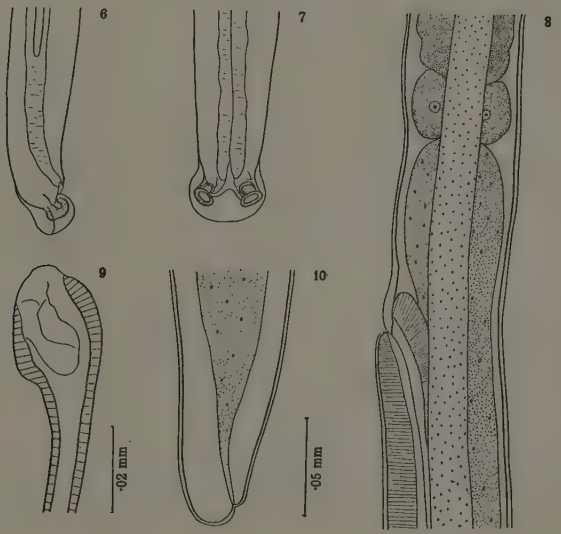
Synonyms *Trichosoma columbæ* Rud., 1819.
Calodium tenue Duj., 1845.
Trichosoma tenuissimum Dies., 1851.
Trichosoma columbæ Neveu-Lemaire, 1912.
Capillaria dujardini Travassos, 1914.

Included in the above list of synonyms is *C. dujardini*, a new name proposed by Travassos (1914) for *Calodium tenue* Duj., 1845. This latter name, however, is antedated by *Trichosoma columbæ* Rud., 1819 which, although not accompanied by a description, can stand for the Capillarid worm of the pigeon as it is, so far, the only species found in this host.

C. columbæ has already been well described and figured by Irwin-Smith (1920) and by Graybill (1924). The present writer has little to add to these accounts and a description is given here chiefly for the purpose of indicating the differences between this species and the other forms found in the domestic fowl.

Female.—The length of the female varies from 10·5 mm. to 14·5 mm. with an average length of 12·5 mm. The region from the head to the posterior end of the œsophagus measures from 4·5 mm. to 6·5 mm. and

is less than half the total length of the body. The width at the head end is about 0·008 mm.; 0·06 mm. at the base of the œsophagus; 0·03 mm. at the anus and a maximum width of 0·08 mm. The vulva is situated about 0·06 mm. behind the junction of the œsophagus and the intestine, a distance which is slightly less than that found in *C. longicollis*.



C. columbæ.

Fig. 6. Tail end of male, lateral view.
Fig. 7. Tail end of male, ventral view.
Fig. 8. Region of vulva, lateral view.
Fig. 9. Anterior end of spicule under high magnification.
Fig. 10. Tail end of female, lateral view.
The left hand scale refers only to Fig. 9.

The vulva does not project so prominently as in the latter species and the absence of a membranous protrusion from the vulva is another characteristic which distinguishes *C. columbæ* from *C. longicollis*.

The body narrows down fairly sharply near the tail end which is

bluntly rounded. The cylindrical character of the tail noted in *C. longicollis* is not found here and this feature serves to distinguish between the females of the two species.

Transverse striations are present and also broad lateral bacillary bands which can be observed along the whole length of the body ; these have a width which is slightly less than half that of the body. There is also a very narrow ventral band present.

The eggs measure from 0·048 mm. to 0·055 mm. by 0·022 mm. to 0·027 mm.

Male.—The length of the male varies from 9·5 mm. to 11·5 mm. with an average length of 10·2 mm. The anterior region has an average length of 5·2 mm. which is slightly more than half the total length of the body. The width at the head end is 0·006 mm. ; 0·048 mm. at the base of the œsophagus ; 0·03 mm. at the cloaca and a maximum width of 0·055 mm.

The spicule has a length of 1·08 mm. to 1·43 mm. and is rounded at the tip while the anterior end is expanded into a knob-like structure. The sheath of the spicule is often extruded and is marked by transverse striations or corrugations but has no spines.

The tail end terminates in a bluntly rounded bursa-like membrane which is supported by two broad L-shaped processes. These are broader and shorter than the same structures in *C. longicollis*. There are no caudal alæ present.

Transverse striations are present and the width of the lateral bacillary bands is between one-half and one-third the width of the body.

As already stated, *C. columbæ* was found to be a very common parasite of fowls in this district and its occurrence also in America, as recorded by Graybill (1924), tends to shew that it has a wide distribution in this host. The possibility, therefore, that *C. longicollis* from the fowl has been, in some instances, mistaken for *C. columbæ* must not be overlooked since both species occur in the small intestine of this host.

C. columbæ has been recorded from *Columba livia domestica, Columba livia, Zenaidura carolinensis, Gallus domesticus* and *Meleagris gallopavo.*

CAPILLARIA RETUSA (Rail., 1893) Travassos, 1915.

Synonyms *Trichosoma retusa* Rail., 1893.
? *Trichosoma longicolle* Duj., 1845.
Trichosoma longicolle Eberth, 1863.
Trichosoma dubium Kowal., 1894.
Trichosoma retusa Kowal., 1901.

Although *T. longicolle* Duj., 1845 is generally referred to as a synonym of *C. retusa* the present writer does not consider that Dujardin's description gives sufficient data to warrant this conclusion. It is true that the worms described by this author are very small when compared with the size given for *C. longicollis* but there is little else to shew that the worm should be referred to *C. retusa*. *T. longicolle* Eberth, 1863 is undoubtedly the same as *C. retusa* since it has a broad ventral bacillary band and was, moreover, found in the cæcum of the domestic fowl.

Female.—The female measures from 11 mm. to 15 mm. in length and the distance from the head end to the posterior end of the œsophagus is from 4·5 mm. to 5·75 mm. which is less than half the total length of the body. The width of the worm is 0·009 mm. at the head end; 0·055 mm. at the base of the œsophagus; 0·035 mm. at the anus and a maximum width in the posterior half of the body of 0·064 mm. About 0·005 mm. from the anterior end an annular constriction is present which, in some specimens, is only faintly indicated and difficult to see even under high magnification. A similar feature is recorded by v. Linstow (1873) in the species *C. collaris*.

The vulva is situated on a slight prominence about 0·063 mm. behind the posterior end of the œsophagus. There is no membranous appendage present at the vulva in the fully grown female but one is occasionally found in immature forms.

The tail end of the female narrows considerably towards the tip and is more like the tail end of *C. columbæ* than that of *C. longicollis*; the tip is bluntly rounded and the anus is sub-terminal.

There is a broad ventral bacillary band present which has a width about half that of the body; lateral bacillary bands are also present but these are much narrower.

The worm is transversely striated.

The eggs are rugose and measure 0·055 mm. to 0·057 mm. by 0·025 mm. to 0·029 mm.

Male.—The length of the male is from 8 mm. to 13 mm. and the proportion of the anterior region to the total length is as 2 : 5. The width is 0·007 mm. at the head end; 0·04 mm. at the base of the œsophagus; 0·03 mm. at the cloaca and the maximum width is 0·05 mm.

The spicule has a length of 1·23 mm. to 1·4 mm. and is bluntly rounded at the tip; it shews three longitudinal thickenings and short transverse markings. The anterior end is much broader than the tip and reaches a width of 0·02 mm. It does not form a knob-like structure as in *C. columbæ* but is bluntly conical.

The spicular sheath is often extruded and is covered with spines which are directed anteriorly.

The tail end is bluntly rounded and terminates in a bursa-like membrane which is bi-lobed and is shorter than that found in the males of the other two species described in this paper. It is supported by two very short processes which are somewhat L-shaped.

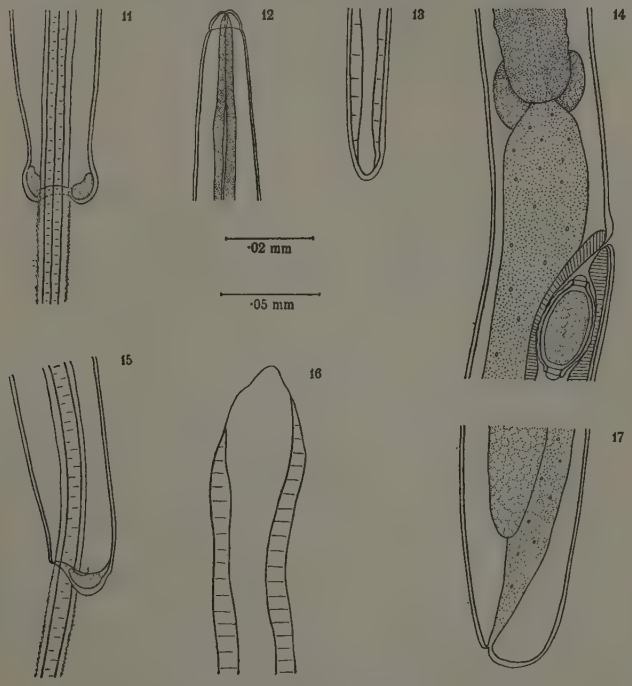
The ventral bacillary band is a little broader in relation to the width of the body than is the case in the female.

C. retusa has been recorded from *Gallus domesticus* and *Numida meleagris.*

The lengths given above for *C. retusa* are slightly less than those given by Railliet (1893), but are, however, somewhat similar to those given by Kowalewski (1895) for the same species. Railliet also states that the sheath of the spicule is smooth whereas, according to Kowalewski who examined some of Railliet's material, there are spines present on this organ.

In comparing the descriptions given for *C. retusa* with those for *C. collaris* (v. Linst., 1873) the present writer is strongly of the opinion that these two species are synonymous. This view is supported by the fact that the annular constriction found in *C. collaris* is shewn in this paper to be present in *C. retusa* also. There is, however, one important feature in which these two species differ, namely in the presence of the broadest bacillary band in a lateral position in *C. collaris* and ventral in

C. retusa and before one can consider the species identical one must assume that v. Linstow either failed to see the ventral band in *C. collaris* or that his material consisted of more than one species. The bacillary bands are certainly difficult to see clearly in some specimens and where, as in the domestic fowl, several species of *Capillaria* occur the latter possibility can be readily understood.



C. retusa.

Fig. 11. Tail end of male, ventral view.
Fig. 12. Head end shewing annular constriction.
Fig. 13. Tip of spicule under high magnification.
Fig. 14. Region of vulva, lateral view.
Fig. 15. Tail end of male, lateral view.
Fig. 16. Anterior end of spicule under high magnification.
Fig. 17. Tail end of female, lateral view.
The upper scale refers to Figs. 12, 13, and 16.

Capillaria annulata (Molin, 1858).

Unfortunately, no material could be obtained for a detailed study of *C. annulata* but from the descriptions given in the literature it is clear that this is different from the other species found in the fowl. Apart from the fact that it is found in the crop and the œsophagus, this species has a cuticular inflation at the head end which is characteristic. In the structure of the male tail and the character of the spicular sheath it appears to resemble *C. retusa*; it has, however, a much greater length than the latter species.

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Journal of Helminthology, Vol. x, *No.* 4, *September*, 1932, *pp.* 195-208.

Hexylresorcinol as a General Vermicide.

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Introduction.

During recent years the compounds belonging to the resorcinol series have acquired considerable importance as germicides, and among these compounds the hexyl derivative has provided the optimum working value. While this is reasonably active, a sufficient quantity can be obtained in solution for administration.

Leonard and Wood, in 1924 and 1925, proved its efficiency as a bactericide for the urinary tract. As early as 1920 it had been mentioned by Hall and Wigdor as an anthelmintic, but it was not seriously considered as such until 1930 when experiments carried out by Lamson, Ward and Brown proved its efficacy as an ascaricide in dogs. More recently still, these same workers, in conjunction with Caldwell, have used it successfully in human cases, and with Robbins have shown its utility in hookworm infestation.

In a paper published by Wright, Bozicevich and Underwood in 1931 there is definite evidence of its use in the treatment of Nematode parasites in pigs—in particular, *Ascaris*, Whipworms and Nodular worms (*Œsophagostomum*). The pigs were starved first, and after administration of the drug in hard gelatine capsules, castor oil was given as a purge. In some cases all the worms were eliminated and in most a large percentage were removed with a single treatment.

The evidence as to its efficiency in removing Nematodes is conclusive, but there is no general agreement as to the technique to be used nor of the pathological changes produced by it. It is generally administered in hard

gelatine capsules—the trade product being known as Caprokol—each capsule containing 0·15 gm. of hexylresorcinol in a 25 per cent. solution of olive oil.

Lamson, Ward and Brown in 1930 stated that certain pathological conditions were associated with hexylresorcinol administration, in particular small submucosal hæmorrhages and focal necrosis of the epithelium. Wright and his collaborators found no such changes, however. Some of the pigs showed cloudy swelling of varying intensity and an acute nephritis, but the degree of intensity could not be correlated with the size of the dose and hence they assume that the lesions were not produced by the action of the drug. These are two very divergent views and various intermediate opinions have been expressed. The findings of the present writer will be noted later in this paper.

The drug is rapidly gaining a reputation as an efficient vermicide and has been used experimentally to a large extent among the Nematodes, where it seems to be equally good in infestations of *Ascaris* and Hookworm and to a less extent on Whipworm and *Œsophagostomum*.

During the last few weeks the present writer has been experimenting with it as a general vemicide and in this connection has used representatives of all the main biological groups of helminths.

She would particularly like to thank Professor R. T. Leiper, F.R.S., for suggesting the work and for much helpful criticism and advice.

Material.

Both Platyhelminths and Nemathelminths were used and particular attention has been given to ova and larval stages of parasites of economic importance, while free living forms and plant parasites have not been neglected. Previous work has been limited almost entirely to adult parasitic Nematodes, but in this paper there is an attempt to link up all types of helminths, and the experimental evidence is suggestive that it may be as useful in Cestode infestations as in Nematode.

A stock solution of a dilution of 1 : 1000 of n-hexylresorcinol was made up in 0·1 per cent. methyl alcohol. The addition of alcohol was necessary for solution, though the presence of it increased the toxicity of the drug, helping to carry it more readily through the cell membranes. From this stock solution were made up other solutions with dilutions of 1 : 5,000,

1 : 10,000, 1 : 15,000, 1 : 20,000. These same dilutions were used throughout the whole series of experiments.

A. Experiments with Free Living Eelworms.

Three forms, *Rhabditis succaris*, *Diplogaster striatus* and *Dorylaimus saprophilus* were used here. In each case the specimens were removed from cultures which had been running in the laboratory for some time, and all were healthy. A large number of worms were isolated in a minimal amount of water. Some were removed with a fine pipette and added to a large quantity of the drug solutions. In these solutions they all re-acted in a similar manner. For about a second or so they were stunned and lay stretched out ; then followed a period of intense activity. The worms endeavoured to remove themselves from the neighbourhood of the irritant by rapid and jerky muscular contractions of the whole body, but these movements gradually decreased and finally ceased as death supervened. Examined under a low magnification, the worms were seen to be lying very much contracted and in awkward attitudes at the bottom of the dish.

Dilution.	1 : 1,000	1 : 5,000	1 : 10,000	1 : 15,000	1 : 20,000	Controls in 0·1% methyl alcohol
Rhabditis dead in	1 min.	2 mins.	4 mins.	15 mins.	27 mins.	Still alive after 2 days
Diplogaster	1 min.	5 mins.	26 mins.	45 mins.	80 mins.	2 days
Dorylaimus	3 mins.	7 mins.	12 mins.	20 mins.	29 mins.	3-4 days

The drug acts as a protoplasmic poison and the protein matter is precipitated within the cells and appears black and opaque. The cuticle generally swells up to some extent, and in a few cases has actually ruptured, allowing the internal organs to escape.

The results are summarised in the accompanying table, and it will be seen that even in high dilution the drug is very toxic, causing death in a short time ; the controls in 0·1 per cent. methyl alcohol lived normally.

The free living stages of *Strongyloides stercoralis* and *Ancylostoma duodenale* were similarly treated, and the results showed considerable agreement with those obtained from soil eelworms.

Dilution.	1 : 1,000	1 : 5,000	1 : 10,000	1 : 15,000	1 : 20,000	Controls
Ancylostoma rhabditiform	3 min.	12 mins.	30 mins.	45 mins.	60 mins.	3-4 days and then metamorphosed
Ancylostoma filariform	12 mins.	27 mins.	1hr. 40min.	2hr. 45min.	5 hrs.	Many days
Strongyloides rhabditiform	3 mins.	12 mins.	27 mins.	40 mins.	1hr. 15min.	3-4 days and then metamorphosed
Strongyloides filariform	25 mins.	38 mins.	1hr. 12min.	3hr. 10min.	5hr. 30min.	Many days.

Remarkable agreement occurs between the two rhabditiform stages, as also between the two filariform stages, but the older larvæ definitely have a higher resistance. In both cases, however, they can be considered as directly comparable to the free living forms.

B. Experiments with Parasites of Plants.

Infected soil and cysts of *Heterodera schachtii* and *radicicola* were kindly provided by Dr. M. J. Triffitt for experimentation. Free larvæ were obtained and treated with the drug. In the case of *H. schachtii*, the cysts were treated with potato root extract and the larvæ hatched naturally ; for *H. radicicola*, the larvæ were dissected from cysts attached to tomato roots.

Dilution	1 : 1,000	1 : 5,000	1 : 10,000	1 : 15,000	1 : 20,000	Controls
H. schachtii	2 hrs.	12 hrs.	3 days	13 days.	more than 16 days	Many days
H. radicicola	2 hrs.	20 hrs.	45 hrs.	2½ days.	3 days	4-5 days

The larvæ of *H. radicicola* are more readily attacked than those of *H. schachtii* which show a very noteworthy resistance. A similar re-

sistance to most dyes and various other substances has already been noted, and hence this particular immunity is perhaps not unexpected. In the solutions of greatest dilution, the activities of the worms seemed to be unimpaired for they continued to live as actively in this medium as did the controls in tap water. They were abandoned after 19 days, but at that time they differed in no way from the controls. A few deaths had occurred after eight or nine days, but these were probably from natural causes and they were counterbalanced in the control watch glasses.

The permeability of the *schachtii* cysts was also examined. It is known that these are easily permeated by certain substances, e.g., hatching is brought about in the presence of dilute potato root extract. Cysts were allowed to remain in the solutions of the drug for 24 hours after which they were transferred to potato root extract. In all cases the larvæ hatched from the cysts in one to three days, while the controls, which had been in tap water before root extract, also began to hatch after 24 hours. The drug therefore fails to penetrate the cyst, and is therefore incapable of inhibiting the hatching process; the larvæ which hatched were in no way affected, but behaved normally in every respect. Hatching was slow for about two days, but later it speeded up so that there were always large numbers of larvæ available.

C. Experiments with Animal Parasites.

1. *Trematoda.* Living ova of *Schistosoma hæmatobium* were obtained and treated with the drug, but the diluent in this case was fresh urine. Leonard has shown that the toxicity of the drug is in no way lessened when urine is the diluent, though when the drug is taken by the mouth much is excreted in the stool, and of that appearing in the urine a large percentage is "fixed" and not available for germicidal or bactericidal purposes. The solutions used in this experiment were of the same dilution as had been used in water for the Nematodes.

Eggs with actively moving miracidia were isolated from the urine, placed in the drug solutions and observed under the microscope. The shell is very permeable and the enclosed miracidia were rapidly affected by the poison. In the solutions of least dilution the substance diffused through the shell almost immediately, and even in greatest

dilution the larvæ were affected in a few minutes and died shortly afterwards. They reacted strongly to the presence of the toxic substance ; when it came into contact with the body, the superficial cilia were strongly stimulated and endeavoured to ward off the poison. The body contracts violently and finally the cilia are paralysed and stand out stiffly from the body surface. Penetration into the deeper tissues does not occur for three to six minutes, according to the dilution. The flame cells form a reliable index of the rate of penetration ; they are first stimulated and later paralysed and not until they had ceased moving was the miracidium considered to be dead.

The dead larvæ, as with the Nematodes, were considerably mutilated as a result of the violent muscular contractions and blackening and precipitation of the protoplasm. The controls lived in urine for several hours. In the next experiment the miracidia were hatched in tap water and treated with aqueous solutions of hexylresorcinol. In all dilutions, death occurred rapidly and the symptoms already catalogued were observed.

Similar experiments were carried out on the eggs of *Fasciola hepatica* obtained from a sheep with a heavy infestation. The shells being much thicker than those of *Schistosoma hæmatobium*, penetration was of necessity slowed down. A large number of ova were isolated in watch glasses and remained in contact with the drug for 24 hours, after which they were washed and transferred to tap water. The hatching processes were observed. In some cases the larvæ had tried to hatch while the eggs were in the drug solution, but none had survived the toxic effects long enough to escape completely from the shell.

In a solution of dilution 1 : 1,000, sufficient penetration had occurred into all the eggs to inhibit development completely. Contained larvæ were contracted within the egg, while the contents of the eggs in earlier stages of development were blackened and coagulated. Though left in tap water at a favourable temperature for several weeks, no further development occurred. In the other solutions, penetration had occurred into some of the eggs, but it was not easy to estimate the percentage mortality. Only in cases of advanced development could one be certain that death had occurred ; in earlier stages much conjecture was necessary. Further, even in the control watch glasses which contained water always,

a large percentage of ova failed to develop. It was quite definite, however, that a certain number had been affected, and this number decreased as the dilution increased.

Free miracidia were treated directly with the drug, and these proved very susceptible. They reacted in a manner similar to the *Schistosoma* miracidia and died after a short exposure. The results are summarised in a table.

Dilution	1 : 1,000	1 : 5,000	1 : 10,000	1 : 15,000	1 : 20,000	Controls
Schistosoma enclosed miracidia	30 secs.	1 min.	2 mins.	8 mins.	12 mins.	Some hours
Schistosoma hatched miracidia	immediately		1 min.	2 mins.	2 mins.	Some hours
Fasciola hatched miracidia	immediately		1 min.	1½ mins.	2 mins.	Some hours

The penetration of the drug into *Fasciola* eggs when bile was the diluent was considered. The drug went into solution easily owing to the alkaline reaction of the bile, but very little data was obtained. The eggs had been in the laboratory for some time before a sufficient quantity of bile could be obtained, and hence were stale ; even the controls which remained in pure bile for 24 hours before being transferred to tap water, failed to develop.

As has already been noted, a solution 1 : 1,000 of the drug proved toxic to a very high percentage of *Fasciola* eggs. The rate of penetration of such a solution was examined. Embryonated eggs were carefully isolated and washed before treatment. The permeability of the shell varies considerably, but some are sufficiently permeable for the enclosed larvæ to be killed within three hours. After seven hours all the larvæ had been killed and at any time after three hours, there could be seen larvæ which were contracting or otherwise resisting the toxic action of the drug. Death supervened usually between five to twelve minutes after muscular contractions were definitely established.

2. *Cestoda.*—Results obtained with ova of *Dibothriocephalus latus* agreed very closely with the *Fasciola* results ; penetration occurred in

about the same time and only a few of the ova were able to continue their development after treatment. Living onchospheres were killed in a few minutes.

These free living larvæ naturally prove very susceptible to the action of the drug. Their bodies are very delicate—much more so than the free living Nematodes which have a comparatively thick layer of cuticle for protection.

A mouse with a heavy natural infestation of *Hymenolepis murina* was available, but died before any treatment could be given. At autopsy 10 fully mature worms were recovered from the gut ; it is interesting to note that they were all located close together, shortly behind the cæcum, instead of in the usual position in the small intestine.

These were removed immediately after the death of the mouse and used in some *in vitro* experiments. Solutions of the drug were made up in physiological saline and the experiments carried out at blood temperature in an incubator. Worms of roughly similar length—about 1 inch—were used for immersion in these solutions. Death occurred very rapidly while the control worms in saline remained alive for several hours.

Dilution 1 : 1,000—death occurred within 1 minute.
„ 1 : 5,000— „ „ „ 2 „
„ 1 : 10,000— „ „ „ 4 „
„ 1 : 15,000— „ „ „ 4 „
„ 1 : 20,000— „ „ „ 5 „

Eggs were removed from the gravid segments of another piece and treated for 24 hours with resorcinol. After having been thoroughly washed they were fed to mice with the following results :—

Resorcinol Solution.	Eggs fed to Mouse.	Result of Infestation.
1 : 1,000	A.	Negative.
1 : 5,000	B.	„
1 : 10,000	C.	„
1 : 15,000	D.	Positive.
1 : 20,000	E.	„
Untreated controls.	F.	„

Mice A and B withstood the experiment and remained uninfected; mice D, E and F also withstood the experiment, but became infected with *H. murina*. Deposition of eggs began about 25 to 30 days after feeding. Mouse C died 25 days after feeding, the cause of death being a bacterial infection. The intestine was carefully examined, but there was no trace of any young *Hymenolepis* either with the naked eye or by means of sections. It is not unreasonable to suppose, therefore, that there was no infestation here either.

The mice used here were all adult, weighing on an average 29 gm., and as Woodland found when attempting infestations with "*H. fraterna*," young mice are more easily infected than older ones; 90 per cent. young mice being infected as against 23·3 per cent. older ones. Had young mice been used, therefore, some of the others might have taken the infection, but from these results one can infer that the stronger solutions of hexylresorcinol proved lethal to all the ova. Greater dilution reduces the toxicity and some ova are able to withstand it and remain viable. When these are fed to a suitable host, some of these viable eggs develop into adult *H. murina*.

The only *in vivo* experiments were carried out with mice infested with *Hymenolepis murina*.

A solution of the drug was made up in olive oil of such a strength that 1 cc. of the solution contained 0·01 gm. of the drug. This was fed to the mice mixed with a small quantity of bran. Previous complete starvation was avoided though no food was taken for 7 to 8 hours previously and a meal followed about two hours after treatment.

Mouse 1.—Dose 0·05 gm. Several tapeworms were passed. The animal died 24 hours after administration of the drug. No living worms were recovered at autopsy, but there were many dead *Aspicularis sp.* lying in the lumen of the intestine and cæcum. The blood vessels were congested and the mucosa was inflamed; in parts it had sloughed away from the underlying tissues. Some cloudy swelling of the liver parenchyma was noticed.

Mouse 2.—Dose 0·04 gm. Several *Hymenolepis* and some *Syphacia sp.* passed. The mouse died four days after administration of the drug. At autopsy the intestine and cæcum were negative for all helminths. The

mesenteric and vesical vessels were congested and there had been some small hæmorrhages into the small intestine. The stool was bloodstained.

Mouse 3.—Dose 0·03 gm. Several *Hymenolepis* and a large number of *Aspicularis* were passed. The stool was examined at intervals for six weeks afterwards and proved negative for all helminth eggs.

Mouse 4.—Dose 0·02 gm. Pieces of *Hymenolepis* passed and two days later the stool was negative for all helminth eggs and remained so during four weeks of examinations.

Mouse 5.—Dose 0·01 gm. Many pieces of *Hymenolepis* were passed. Two days later the stool contained a large number of *Hymenolepis* ova. A second administration of 0·01 gm. of the drug was given, and a large piece of worm was passed. For two days the stool was negative for eggs, but later deposition began again, showing that some Cestodes still remained.

Mouse 6.—Dose 0·005 gm. Small portions of worm were passed together with some *Syphacia*. The stool was free from eggs for 24 hours, after which both *Hymenolepis* and *Syphacia* ova appeared.

The technique used here differed from that used by previous workers in that complete starvation was avoided and no purge was administered afterwards. The drug certainly combines with proteins lying free in the gut, but it was felt that starvation would be detrimental to the health of the animals and to its natural reserves, and that hence the results would not be a clear index of the potency and toxicity of the drug.

Pathological Changes.

Notice has already been taken of the pathological lesions produced by Lamson, Ward and Brown in dogs and of the fact that Wright and Underwood are in complete disagreement with these results from their work on pigs. The results of the present writer agree fairly closely with those of Lamson and his co-workers.

At autopsy, mice treated with hexylresorcinol, showed certain general changes. The mesenteric and vesical vessels were in all cases much congested; after a heavy dose, there were small petechial hæmorrhages occurring into the intestine along its whole length, and particularly into

the small intestine. A large quantity of mucus was being secreted and excreted with the stool; the mucosa was sometimes damaged.

These appearances were all visible to the naked eye. For more detailed histological changes, sections of various organs, in particular, the liver and kidney, duodenum and bladder were made. For these a mouse was given several small doses followed by a large dose of the drug, sufficient to bring about death in 12 hours. The lesions were, therefore, pronounced, but there is no reason to suppose that they differed in any respect, other than that of degree, from those produced by a clinical dose.

The sections of the duodenum showed the same lesions as had already been observed at autopsy. In addition, the capillaries were hyperæmic and many smaller hæmorrhages were visible in the submucosa, in which region there was also a diffuse inflammation. The globet glands in the crypts of Lieberkühn showed a particularly marked increase in activity. The epithelium showed no marked changes except in the regions where the mucosa had sloughed away, but remained intact with a healthy appearance.

Some resorcinol is excreted by the kidneys and, as a result of the passage of the drug, the tubules showed some small lesions. The general appearance of the kidney was healthy, but in sections there could be seen small necrotic foci in the cortex. Some slight degree of fatty degeneration was visible in the convoluted tubules, but Bowman's capsules and enclosed glomeruli were unaffected. There was a slight infiltration of round cells, mainly of the polynuclear variety, in the neighbourhood of the convoluted tubules.

The bladder showed very little change. There was some inflammation in the submucosa, but there were no hæmorrhages and no histological changes in the epithelium.

Well marked changes occurred in the liver. The organ was somewhat greasy to the touch and very fragile. On cutting into it, unusually heavy bleeding occurred due to the fact that the portal veins were congested. Sections showed pronounced fatty changes; cloudy swelling was seen all over the section together with foci of fatty degeneration. An intense infiltration with polymorph leucocytes had taken place into Glisson's capsules and along the interlobular connective tissue strands.

The blood in the peripheral circulation appeared normal and there were no obvious changes in the shape or size of the erythrocytes.

Though well marked changes occur in essential tissues—mainly fatty changes and an inflammatory reaction—yet they are not so profound as to preclude regeneration on a return to normal conditions.

Conclusions.

Hexylresorcinol appears to be as effective as a vermicide as a bactericide. The work carried out by Lamson and his collaborators in America has shown it to be useful in removing some Nematodes. The present writer has obtained similar good results with Cestodes and experiments on free living Eelworms and larvæ of parasitic Nematodes show that it is extremely pathogenic to these also.

In each case the drug acts as a protoplasmic poison by precipitating the protein contents. For this reason it does not penetrate deeply into the tissues though its permeability and hence its toxicity is increased by solution in alcoholic or alkaline solutions.

According to results obtained in America by Henline in human bacterial infections of the bladder and by Lamson and his collaborators in canine ascariasis, mammals seem able to withstand comparatively large doses of the drug. If, however, an overdose is administered, it causes congestion of the mesenteric and vesical vessels, and in certain cases severe petechial hæmorrhages into the lumen of the intestine. The mucosa is frequently sloughed. Increased secretion of mucus always occurs after administration even when only a small dose has been taken. Cloudy swelling and fatty degeneration of the liver parenchyma and necrotic foci in the kidneys have been observed.

Comparatively small doses are effective in removing all helminths from the digestive tract. What is perhaps of greater importance is that both ova and adults are killed and hence there is no danger of further irritation of the intestine by wanderings of the parasite or infestation lower down in the gut.

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Journal of Helminthology, Vol. x, No. 4, September, 1932, pp. 209-230.

On a Collection of Parasitic Worms from East Africa.

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The following material was sent to the Department of Helminthology of the London School of Hygiene and Tropical Medicine in three groups; two lots coming from Mr. Aneurin Lewis, of the Veterinary Research Station at Kabete, Kenya Colony, and the third lot from the Director of Veterinary Services, Uganda. For this latter, the writer is indebted to the Imperial Bureau of Agricultural Parasitology. The major part of the material was placed at his disposal by Professor R. T. Leiper, F.R.S., to whom he wishes to express his sincere thanks.

The material comprises three species of Trematodes, 19 species of Nematodes and 13 species of Cestodes, as well as certain immature worms. Of these, one Nematode and one Cestode are considered to be new to Science, and are accordingly described in some detail.

In view of the rising importance of Animal Industry in East Africa, and of the significance of African game as reservoir hosts for parasitic infections, the collection is here described in full, with such references as could be found to previous records of the occurrence of these species in Africa.

TREMATODA.

The collection comprises three genera of flukes representing three families.

Fam.: *FASCIOLIDÆ* Railliet, 1895.

Genus: Fasciola Linn, 1758.

Fasciola gigantica (Cobbold, 1856). There are three bottles of this fluke taken from oxen and cows at Kabete, Kenya. It is a well-known

parasite of the biliary tract of herbivora, and its occurrence in East Africa is discussed by Jackson (1921, p. 48) in his revision of the genus *Fasciola*.

Fam.: *PARAMPHISTOMIDÆ* Fischœder, 1901.

Sub-fam.: *PARAMPHISTOMINÆ* (Fisch., 1901), Stiles and Goldberger, 1910.

Genus: COTYLOPHORON Stiles and Goldberger, 1910.

Genus erected for Paramphistomes without pharyngeal diverticula, but with a genital sucker.

Cotylophoron cotylophorum (Fischœder, 1901), S. and G., 1910, is a parasite of cattle and antelopes in Africa. It was first discovered in German East Africa. Maplestone (1923, p. 151) records it from a number of African Ungulata including *Bubalis* sp., *Cobus* sp., *Æpyceros melampus* and various forms of cattle. The specimens in this collection are from an ox at Bunyoro, Uganda. Maplestone's records are from Sierra Leone, Nigeria, Nyasaland, Rhodesia and the Sudan. Le Roux (1930, p. 243) records this worm from sheep in the Orange Free State and contributes experimental data concerning its life history there. It appears to be well distributed throughout Tropical Africa as a parasite of ruminants, and apparently antelopes may be regarded as reservoir hosts. The genus is further represented in Africa by *C. minutum* and *C. sellsi*, both recorded from the hippopotamus by Leiper (1910, p. 244).

Fam.: *GASTROTHYLACIDÆ* Stiles and Goldberger, 1910.

The sub-family *Gastrothylacinæ* (S. and G., 1910) is not recognised by Maplestone in his revision of mammalian Amphistomes (1923).

Genus: CARMYERIUS S. and G., 1910.

Amphistomes with a ventral pouch; uterus along the median line, and testes side by side. According to Maplestone (p. 178), this genus is synonymous with *Wellmanius* (S. and G., 1910, p. 51).

The genus is here represented by about ten specimens of *Carmyerius exoporus* Maplestone, 1923 extracted from the rumen of an ox at Thompson's Falls, Kenya. This species is easily diagnosed as the only one in which the genital pore lies outside the ventral pouch. Paraffin sections through the median longitudinal plane are necessary to establish

this point. Maplestone (p. 185) gives a characteristic diagram of such a section. The ventral pouch in these specimens has a thick muscular lining, and shows four to six angles in transverse section, some being extended into single or multiple diverticula. Maplestone's specimens are from the Marsh-buck, *Tragelophus spekei*, in Nyasaland. Stiles and Goldberger erect the Genus (1910, p. 50) for specimens from *Bos bubalis* in Egypt and *B. taurus* in East Africa.

This completes the Trematode material.

CESTODA.

Fam.: *ANOPLOCEPHALIDÆ* Fuhrmann, 1907.

Sub-fam: *THYSONOSOMINÆ* Fuhrmann, 1907.

Genus: STILESIA Railliet, 1893.

Stilesia hepatica (Wolffhügel, 1903), from a goat at Kijabe, Kenya.

Sub-fam.: *ANOPLOCEPHALINÆ* Fuhrmann, 1907.

Genus: ANOPLOCEPHALA Blanchard, 1848.

The genus comprises large tapeworms, mainly from Perrissodactyl Ungulates, and is here represented by two species.

Anoplocephala magna (Abildgaard, 1789). According to Baer (p. 26) this worm is a cosmopolitan parasite of equines. The material consists of a single very fine specimen from Grévy's Zebra (*Equus grévyi*), from Laisimis, Kenya. The Zoological Society's list of mammals (p. 253) gives the host's range as " N.E. Africa and Abbyssinia, extending into Somaliland and B.E.A." The specimen is a stout, thick tapeworm measuring 7 in. long by 1 in. maximum breadth. The scolex measures 5 mm. in diameter and bears no lappets upon its posterior margin.

Anoplocephala perfoliata (Goeze 1782). The specimens are from Grant's Zebra which is not in the Zoological Society's list unless it is *E. burchellii granti*, a form of Burchell's zebra. The worm is a cosmopolitan parasite of donkeys, horses and zebras (Baer., p. 23). The scolex bears upon its posterior margin a dorsal and a ventral pair of blunt lappets which serve to distinguish it from *A. magna*. The locality is the Kilimandjaro district.

The Anoplocephalid material is completed by a complete immature worm from a goat at Kijabe.

Fam.: *TÆNIIDÆ* Ludwig, 1886.

Genus: TÆNIA Linn, 1758.

The only adult tænioid tapeworm in the collection is *Tænia sp.* from the small intestine of a jackal. The locality is Ngong, Kenya. The immature condition of the reproductive organs makes specific diagnosis impossible. The scolex bears two circlets of 16 hooks each. The large hooks measure 160-180μ, and the small ones 100μ long. This is probably either *T. ovis* or *T. hydatigena.*

There are two cysticerci in the collection, viz., *C. cellulosæ* from the muscles of a pig; and *Cysticercus sp.* encysted on the serous surface of the intestine of a spitting cobra (*Naja nigricollis*). The occurrence of *C. cellulosæ* (at Kabete) is of interest, as the typical tapeworm of man in this part of the world is *Tænia saginata*, the beef tapeworm. The cysts from the spitting cobra are about 2 mm. in diameter, and are situated beneath the thin peritoneal investment of the intestine. They do not appear to have rostellar hooks. The cobra is from Ngong.

Fam.: *DAVAINEIDÆ* Fuhrmann, 1907.

Genus: RAILLIETINA Fuhrmann, 1920.

Sub-genus: *Raillietina.*

Raillietina (*Raillietina*) *tetragona* (Molin, 1858). The material consists of two complete mature specimens from the intestine of a fowl. The locality is Koja, Uganda. The sub-genus *Raillietina* has been proposed to include those members of the original genus, in which the genital pore is unilateral and the egg-capsules contain more than one egg. In addition to these adults a piece of intestine was sent showing a light infection with immature Davaineid worms which have been provisionally assigned to this species. A histological examination of the connective tissue nodules which these parasites set up, revealed a very advanced tissue response involving advanced fibrosis and necrosis in the muscular part of the intestinal wall; pressure atrophy of the serosa; rupture and atrophy of the mucosa and a well marked small round cell infiltration. Each lesion is organised round a scolex which is buried deep in the muscular tissue. The lesions are avascular, and there is no sign of hæmmorrhage. Such a

very advanced tissue response is not usually associated with an infection with young cestodes.

Sub-genus : *Paroniella.*

To this sub-genus are assigned those species of *Raillietina* characterised by irregularly alternating genital pores and more than one egg in each egg-capsule. The writer has provisionally classed as *Raillietina* (*Paroniella*) sp. some badly preserved cestode fragments from a chicken. They appear to show the above characters, but no scolices were present. The fowl was from Kikuyu, Kenya.

Fam. : *ICTHYOTÆNIIDÆ* Ariola, 1899.

Genus : OPHIOTÆNIA La Rue, 1911.

Ophiotænia gabonica (Beddard, 1913). The material is from the intestine of *Bitis* sp. from Ngong, Kenya. Beddard (1913, p. 153) described a Proteocephalid from *Bitis arietans*, under the name *Icthyotænia gabonica*. Sandground (1929, p. 138) describes specimens of *Ophiotænia gabonica* from Amani, Tanganyika, which he considers to be identical with Beddard's *I. gabonica*.

The only other species of *Ophiotænia* which the writer can find recorded from the genus *Bitis* is *O.adiposa*. This is described by Rudin (1917, p. 264) from a snake, which he thinks is *B. arietans*, from the Cameroons. It can be distinguished from *O. gabonica* by the possession of a vestigial apical organ (" fifth sucker ") on the scolex. This character is lacking in the specimens under examinations.

Fam. : *DIPYLIDIIDÆ* Lühe, 1910.

Genus : DIPYLIDIUM Leuckart, 1863.

Dipylidium caninum (Linn.) from a dog at Kabete, Kenya.

Fam. : *HYMENOLEPIDIDÆ* Railliet and Henry, 1909.

Sub-fam. : *HYMENOLEPINÆ* Ransom, 1909.

Genus : HYMENOLEPIS Weinland, 1858.

Hymenolepis multistriata Rudolphi. The specimens of this uncommon species of *Hymenolepis* were taken from the small intestine of a " coot." The locality is Kabete, Kenya. They were first described by the

writer under the impression that they constituted a new species, but subsequently Professor O. Fuhrmann, of Neuchâtel, was kind enough to examine the worms and assign them to this species.

H. multistriata has been described by Cohn (1901, p. 302), who bases his description on specimens from *Podiceps minor*. Professor Fuhrmann considers that the host here referred to as a "coot" was in reality a species of *Podiceps*, i.e., a grebe. While accepting Professor Fuhrmann's diagnosis, there are certain points in which the writer's observations differ from those made by Cohn.

1. The rostellar hooks measure 36μ to 45μ in these specimens, according to the writer's own observations. Professor Fuhrmann makes it 48μ to 50μ. Lühe (1910, p. 76) gives the length as 48μ to 52μ, whereas Cohn gives it as only 15μ. Presumably, Cohn's figure is incorrect.

2. Cohn describes the position of the vitellarium as being ventral to the ovary, whereas in the material examined its position is dorsal to the connection between the two ovarian lobes.

3. Mayhew (1925, p. 40), places *H. multistriata* among those species of avian Hymenolepis in which the two antiporal testes are separated from the poral testis by the female reproductive glands.

In this material the position of the female glands is mid-ventral to the testes which lie close together or are even overlapping, and occupy the middle third of the dorsal half of each segment.

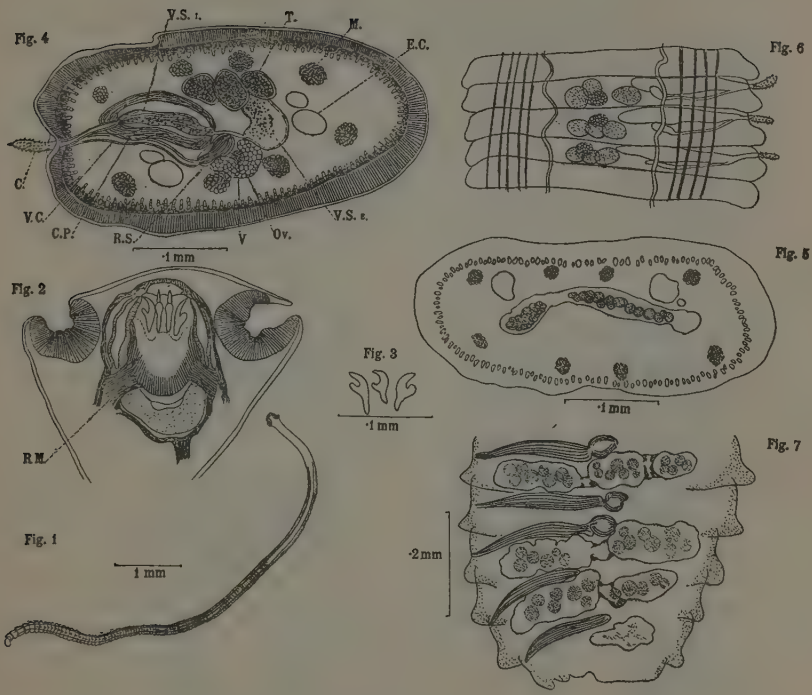
4. Lühe places the genital pore in the middle of the lateral margin of each segment, whereas in these specimens it lies in the antero-lateral corner.

In other respects the observations made correspond fairly closely with those of Cohn. As the latter gives only one inadequate figure, a series of diagrams, illustrating the main points of the worm's anatomy is given. (Figs. 1 to 7.)

Fam.: *AMABILIIDÆ* Fuhrmann, 1908.

Genus: TATRIA Kowalewski, 1904.

This genus of small avian tapeworms is represented in this collection by *Tatria decacantha* Fuhrmann, 1913, and by a species new to Science. The host is the same "coot" (i.e., *Podiceps* sp.) from which the *Hymenolepis multistriata* was taken; apparently all three worms were cohabiting



Figs. 1—7.—*Hymenolepis multistriata* Rud.

Fig. 1.—Young worm, complete.

Fig. 2.—Median longl. section through the scolex. R.M. = Retractor muscle.

Fig. 3.—Rostellar hooks.

Fig. 4.—Transverse section through a proglottis. T=testis. M.=muscle fascicles. E.C.=Excretory canal. V.S.e.=Ext. sem. ves. V.S.i.=Int. sem. ves. C.=cirrus. C.P.=cirrus pouch. V.C.=vaginal canal. R.S.=Receptaculum. Ov.=ovary. V.=Vitellarium.

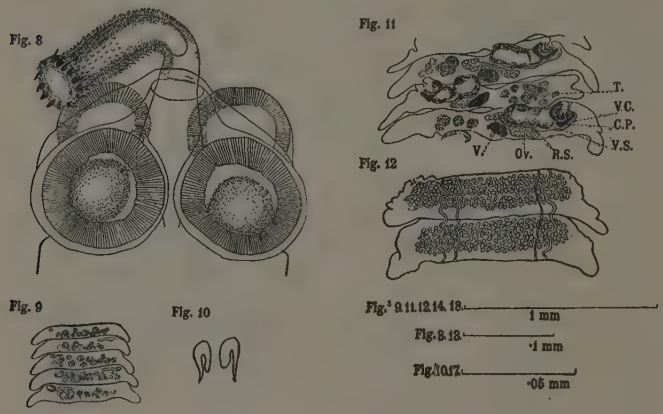
Fig. 5.—Transverse section through a maturing segment showing ova developing *in utero*.

Fig. 6.—Free-hand drawing of testes, ovary and cirrus pouch.

Fig. 7.—Posterior extremity showing gravid segments.

the small intestine. Fuhrmann (1913, p. 36), describes and figures *T. decacantha* so thoroughly that no details are given here. His specimens are from the Crested Grebe (*Podiceps cristatus*) in Sweden. The grebes are migratory birds with a wide range, *P. cristatus* occurring throughout the old world.

The remaining *Tatria* material consists of a single specimen, measuring just over 12 mm. in length. This length includes the scolex, neck and 98 fully formed segments. Sexually mature segments measure 0·06 mm. to 0·15 mm. long by 0·46 mm to 1·4 mm. wide. The gravid segments measure 0·24 mm. long by 0·74 mm. to 1·1 mm. wide. In the middle



Figs. 8—12.—*Tatria fuhrmanni* n. sp.

Fig. 8.—Scolex with evaginated rostellum.

Fig. 9.—Segments showing testis lobes.

Fig. 10.—Rostellar hooks.

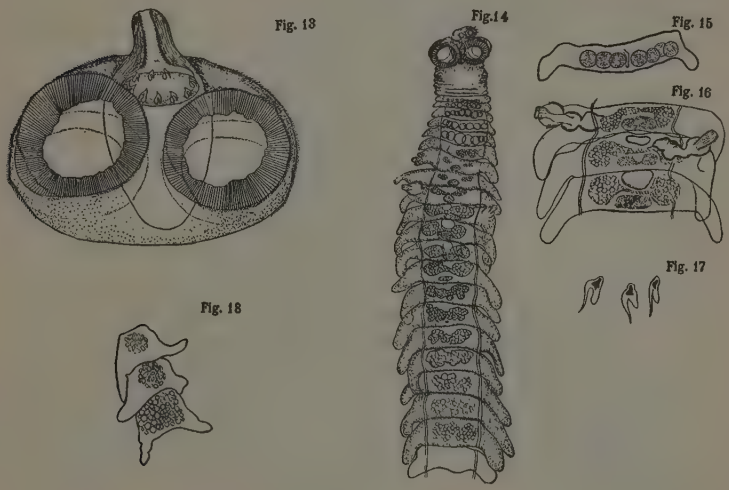
Fig. 11.—Sexually mature segments. T.=testes. C.P.=cirrus pouch. V.=vitellarium. Ov.=ovary. R.S.=receptaculum. V.S.=sem. ves. V.C.=vaginal canal.

Fig. 12.—Gravid segments.

of the strobila the segments have an antero-median constriction making a conspicuous gap between each pair. All well-developed segments have characteristic lateral digitiform processes directed in a postero-lateral direction. The genital pore shows irregular alternation, and is placed at

the anterior corner of each segment. The scolex has a diameter of 0·32 mm. The lumen of each sucker is nearly filled by a plug of connective tissue.

The suckers have a diameter of 0·14 mm. to 0·16 mm. The probosicular rostellum is 0·26 mm. long and terminates in a club-shaped disc bearing a single circlet of 14 hooks (fig. 10), measuring 0·02 mm. long.



Figs. 13—18.—*Tatria decacantha*. Fuhr.

Fig. 13.—Scolex with invaginated rostellum.

Fig. 14.—Complete worm showing sequence of development in different segments.

Fig. 15.—Segment showing mature testes.

Fig. 16.—Segments showing ovary, vitellarium and cirrus.

Fig. 17.—Rostellar hooks.

Fig. 18.—Gravid segments.

(Note.—Figs. 15 and 16 are freehand ; the rest are drawn to scale with camera lucida.)

The stalk of the rostellum is covered by minute bristles directed backwards and measuring 5μ in length. The rostellum sac is 0·12 mm. deep. Segments containing mature testis lobes appear 0·6 mm. behind the scolex. There are 11 to 13 such lobes, which become concentrated on the

aporal side in sexually mature segments. The cirrus is spinose and is evaginated from a muscular pouch. There is a seminal vesicle and a muscular receptaculum, posterior to which lies the ovary. The vitellarium lies mesial to the ovary and the vaginal canal runs outwards from the receptaculum towards the cirrus ; but no vaginal opening is visible and according to Lühe (1910, p. 121) its absence is a characteristic of the genus. The extended receptaculum is pyriform, the broad anterior end overlapping the margin of the preceding proglottis (fig. 11). The uterus is an irregular thin-walled sac (fig. 12). The ova measure 12μ by 8μ *in utero*. There are two pairs of lateral excretory canals.

Affinities. From *T. decacantha* and *T. appendiculata* this species can easily be distinguished by its much greater size and by the possession of 14 rostellar hooks ; from *T. biremis* by both the size and number of the hooks. The only species with 14 hooks of approximately the same length as in this specimen, is *T. acanthocephala*, and this is a broader, shorter worm with only about half the number of testis lobes. Accordingly, the worm under discussion is considered by the writer to constitute a new species and the name *Tatria fuhrmanni* n. sp. is proposed in recognition of Professor Fuhrmann's kind help with this work.

Figs. 8 to 18 contrast the outstanding features of *T. decacantha* and *T. fuhrmanni*. The original specimen is now in the Helminthological Collection of the London School of Hygiene and Tropical Medicine. No previous record of the genus *Tatria* in Africa has been found by the writer.

NEMATODA.

Fam. : *TRICHURIDÆ* Railliet, 1915.

Sub-fam. : *TRICHURINÆ* Ransom, 1911.

Genus : TRICHURIS Rœderer, 1761.

Trichuris spiricollis n. sp. The material upon which this new species is based consists of six females and two males in a rather poor condition of preservation, taken from the cæcum of a Gazelle (*Gazella thompsoni*). The locality is Naivasha, Kenya. Poor preservation having rendered the

worms olive grey in colour and opaque, the details of internal anatomy were elucidated only with difficulty.

The attenuated œsophageal region is tightly coiled like a watch spring, and usually snaps when stretched so that accurate linear measurements

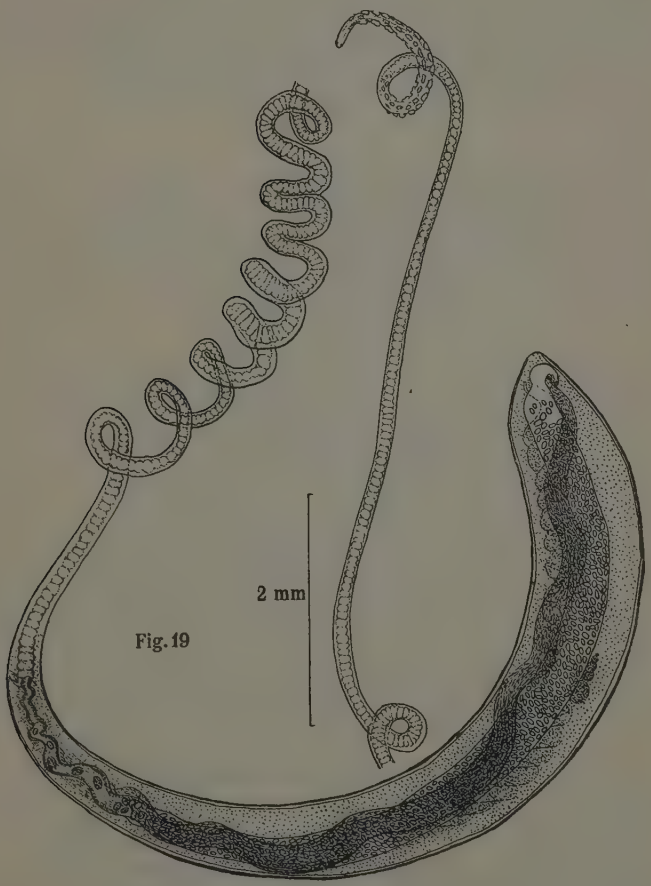


Fig. 19.—*Trichuris spiricollis* n. sp. Complete female.

are not easy to come by. The two male specimens being damaged, measurements of length are taken from the females. The sexes are approximately similar in size, having a length of 27 mm. to 35 mm. The thick part measures 7 mm. to 9 mm. The posterior extremity is straight and blunt in the female, but is twisted into a hook in the male. The slender region constitutes about three quarters or slightly less, of the total length. The greatest breadth in the female is 0·84 mm. The vagina is a winding, muscular tube 0·80 mm. long, opening by a minute vulva close to the base of the cellular œsophagus. There is no vulvar prominence. The ova, as seen in the vagina, measure 0·06 mm. by 0·036 mm., including the polar plugs.

In the male the common cloacal duct is very short, the intestine uniting with the ejaculatory duct 0·2 mm. to 0·3 mm. anterior to the ano-genital opening. The ejaculatory duct measures approximately 0·65 mm. in length and is preceded by a rather wide vas deferens from which it is separated by an indistinct constriction.

The spicule is the most characteristic specific feature. It is slender and measures 1·0 mm. in length (as closely as can be determined for a curved object under the microscope). Anteriorly it bears a small angular knob, and at its posterior extremity it widens out into a spatulate thickening. The dorsal and ventral margins of the spicule are thickly chitinised. The spatulate tip measures 0·024 mm. in breadth. Higher up the spicule narrows to 0·012 mm. wide. The spicule-sheath is covered with small triangular spines directed backwards, except at its tip which is smooth, and, in life, probably swollen, though in the specimens examined it has collapsed (fig. 20). The head measures 0·024 mm. in diameter. The cuticle shows fine annular striations, much sharper in the œsophageal than in the thick part of the body. The distance between each pair of striations is 6μ. The bacillary band is somewhat indistinct.

In the female figured (fig. 19), the cuticle for some distance behind the head shows prominent thickenings, or "plaques," such as are figured by Hall (1916, p. 24), for *T. leporis*. In another specimen examined these "plaques" are replaced by small, clear cuticular vesicles, such as those shown in *T. muris* in the same paper by Hall (p. 26). It seems likely that this is a variable character, at least, for this species.

Affinities. The three outstanding features of this whip worm are: (1) The peculiar spatulate spicule. (2) The spring-like twisting of the œsophageal region. (3) The anterior cuticular "plaques." (4) The very short cloacal duct in the male.

The writer considers that (1), in particular, is characteristic and specific. Schwartz (1926, p. 311), has emphasised the variability of both the spicule and its prepuce-like sheath in the whip-worms of man, swine and primates;

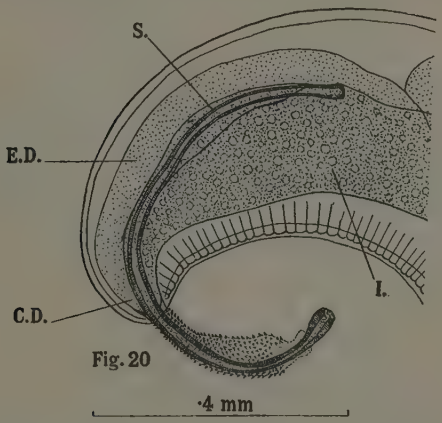


Fig. 20.—*Trichuris spiricollis.* Posterior extremity of male.
I.=rectum. S.=spicule. E.D.=ejaculatory duct. C.D.=cloacal duct.

and has used this point to establish the identity of *T. trichiura* and *T. suis*. Nevertheless, the spicule is here so characteristic that, taken in conjunction with the other characters, it is thought to warrant the erection of a new species.

Apart from the spicule, the posterior extremity of the male somewhat resembles that figured by Barker (1915, p. 195) for *T. opaca*. Chandler (1930, p. 198), has emphasised the significance of the relative size and form of the ejaculatory duct, the cloacal duct and its diverticulum (which is the spicule sheath), in the specific differentiation of whip-worms. As, however,

few previous observers attach any importance to these points, it is difficult to use them for diagnosis. Chandler, in the paper mentioned (pl. xii, xiii), figures the relationship between the genital and alimentary tract in the male of six species of *Trichuris* from all of which the present specimens differ in their abbreviated cloacal ducts. The specific name *T. spiricollis* n. sp. is suggested.

Fam.: *STRONGYLIDÆ* Baird, 1853.

Sub-fam.: *STRONGYLINÆ* Railliet, 1893.

Genus: STRONGYLUS Müller, 1780.

Represented here by the type species *Strongylus equinus* (Müller, 1780), from a horse at Kabete. The genus would appear to be well represented in East Africa. Leiper (1909, p. 26) records *S. equinus* from the East African Zebra at Usambara. Boulenger (1920a, p.27) describes *S. vulgaris*, *S. edentatus* and *S. asinus* from the donkey; and *S. vulgaris* from the zebra, his specimens being from Kenya and Zanzibar.

This genus, as well as the one described next, is a frequent cause of Equine Sclerostomiasis.

Genus: TRIODONTOPHORUS Looss, 1902.

Triodontophorus tenuicollis Boulenger, 1916, from Grant's Zebra in the Kilimandjaro district of Kenya. The material consists of only three specimens and the position in the host is not given. Boulenger erected the species on material from Worcestershire horses.

Sub-fam.: *ŒSOPHAGOSTOMINÆ* Railliet, 1915.

Genus: ŒSOPHAGOSTOMUM Molin, 1861.

The only Œsophagostome in this collection *Œ. columbianum* (Curtice 1890) from a sheep at Nanyuki, Kenya. Boulenger (1923, p. 118) records it from sheep and goats in Zanzibar. Daubney and Carman also mention it in a paper on East African Helminths (1928, p. 187) referring to an unpublished paper by Veglia.

Fam.: *TRICHOSTRONGYLIDÆ* Leiper, 1912.
Sub-fam.: *TRICHOSTRONGYLINÆ* Leiper, 1908.

Genus: OSTERTAGIA Ransom, 1907.

Ostertagia ostertagi (Stiles, 1892) from the abomasum of a goat at Kijabe, Kenya.

Genus: HÆMONCHUS Cobb, 1898.

Hæmonchus contortus (Rud., 1803) from the fourth stomach of a sheep at Rumuruti, Kenya. These two common and cosmopolitan parasites require no further attention here.

Fam.: *ANCYLOSTOMIDÆ* (Looss, 1905) Lane, 1917.
Sub-fam.: *NECATORINÆ* Lane, 1917.

Genus: BUNOSTOMUM Railliet, 1902.

Bunostomum trigonocephalum (Rud., 1808), from a goat. Locality, Kijabe. Here represented by a single male specimen. In their paper, mentioned already, Daubney and Carman (1928, p. 189) refers to this parasite as the cause of hookworm disease in sheep in Kenya.

Fam.: *ASCARIDÆ* Baird, 1853.
Sub-fam.: *ASCARINÆ* (Railliet and Henry, 1912) Travassos, 1913.

Genus: POLYDELPHIS Dujardin, 1845.

Polydelphis attenuata (Molin, 1858). The specimens are from the intestine of *Bitis* sp., from Ngong, Kenya. Baylis (1920, p. 420) has already recorded this worm from *B. arietans* in Africa. The python is another frequent host. The worm has also been recorded from India and (?) the Malayan region.

Sub-fam.: *ANISAKINÆ* Railliet and Henry, 1912.
Genus: PORROCÆCUM Railliet and Henry, 1912.

Porrocæcum angusticolle (Molin, 1860) Baylis and Daubney, 1922. The specimens here described are from the small intestine of a "Rain Eagle" from Ngong. The specific diagnosis is not above doubt. The specimens give the following measurements: Length, male 60 mm. to 70 mm., female up to 80 mm. In a specimen 80 mm. long the œsophagus was

4·1 mm. long, the ventriculus 0·65 mm. long, and the cæcum 3·0 mm. The cæcum varies from 2·5 mm. to 3·0 mm. in different specimens. The œsophagus varies from 4·4 mm. to 4·8 mm. (including the ventriculus), and so constitutes about 1/15th of the total length. The male tail is 0·18 mm. to 0·2 mm. long, and has 15 pairs of precloacal, and four to five pairs of post-cloacal papillæ, one pair of which is double. The spicules measure 0·4 mm. to 0·6 mm. in length. The lips have dentigerous margins. These measurements come fairly close to those given by Cram (1927, p. 137), except as regards the spicules which Cram describes as being 0·95 mm. long. The same writer records *P. angusticolle* from various Accipitrine birds (genera : *Buteo*, *Falco*, *Circus*) from Africa as well as from Eurasia. The exact genus to which " Rain Eagle " should be assigned is uncertain. The worms are provisionally placed under this species.

Fam. : *HETERAKIDÆ* Railliet and Henry, 1914.

Sub-fam. : *HETERAKINÆ* Railliet and Henry, 1912.

Genus : ASCARIDIA Dujardin, 1845.

The collection contains three species of *Ascaridia* as well as one immature female specimen which cannot be identified.

Ascaridia styphlocerca (Stossich, 1904) R. and H., 1914, from a fowl. Locality, Koja, Uganda. The worms are from the small intestine. Diagnosis is based chiefly on the male caudal papillæ. This species has been previously recorded from Africa (Gambia and S. Africa) by Cram (1927, p. 101).

Ascaridia galli (Schrank, 1788) Freeborn, 1923, from a fowl at Kikuyu, Kenya.

Ascaridia columbæ (Gmelin, 1790) Travassos, 1913. The host is given as " a pigeon, Colymbus " from Ngong. As *Colymbus* is a genus of divers, it is assumed that this should read *Columba*, especially as *A. columbæ* occurs in several species of *Columba*, but is not recorded from any species of *Colymbus* (Cram, 1927, p. 87.) It is of world-wide distribution.

The unidentified immature female *Ascaridia* is from the gizzard of a Rain Eagle. Locality, Ngong.

Fam.: *ATRACTIDÆ* Travassos, 1919.

Sub-fam.: *CROSSOCEPHALINÆ* Yorke and Maplestone, 1926.

Genus: CROSSOCEPHALUS, 1909.

This genus occurs in Perrissodactyl Ungulates in the old world. It is here represented by about 25 specimens from a Grant's Zebra. These are considered to be *Crossocephalus viviparus* (Linstow, 1899).

Yorke and Southwell (1920, p. 127) record *C. zebræ* n. sp. from Burchell's Zebra in Northern Rhodesia and give a fully illustrated description. Yorke and Maplestone, however, subsequently record only a single species, *C. viviparus*, from zebras, placing *C. zebræ* in synonymy (1926, p. 250). G. Theiler (1924, p. 684) describes *C. zebræ* and *C. viviparus* as two distinct species, both from equines in South Africa.

Gedœlst (1916, p. 33) records *C. viviparus* from *Equus burchellii crawshayi* at Katanga, Belgian Congo, and is responsible for the taxonomic position of the genus. Accepting that *C. viviparus* and *C. zebræ* are synonymous, this species is then the only African *Crossocephalus*, the other species occurring in Asiatic rhinoceroses.

Fam.: *SPIRURIDÆ* Oerley, 1885.

Sub-fam.: *SPIRURINÆ* Railliet, 1915.

Genus: HABRONEMA Diesing, 1861.

There are two species of *Habronema* in this collection.

Habronema muscæ (Carter, 1861) from a horse. Locality, Kabete. Only a single damaged specimen.

Habronema sp. inq. ? ficheuri (Seurat, 1916). The material so described consists of three females and one male of a somewhat enigmatic *Habronema* from the gizzard of a "Rain Eagle" from Ngong. The females measure 7 mm. to 8 mm. and the males 6 mm. to 7 mm. in length. In the female the œsophagus measures 3·36 mm., i.e., nearly half the total length. Of this, the anterior portion measures 0·3 mm. The buccal capsule is 30μ in depth. The female tail is 0·17 mm. long and the vulva is near the middle and is not prominent.

The lips and cuticular striations closely resemble those figured by

Cram, for *H. ficheuri* (p. 175). This species is from *Bubulcus lucidus* (an egret) in N. Africa. The male tail is slightly twisted. The spicules measure 0·91 mm. and 0·21 mm. respectively. There are caudal alæ supported by papillæ, and there is a small group of sessile papillæ near the posterior extremity which terminates in a small conical spine. The male has a single lateral ala, but the female has none. According to Cram, alae are entirely absent in *H. ficheuri* from which these specimens also differ in size, being considerably smaller.

Genus: SPIROCERCA Railliet and Henry, 1911.

Several nodules excised from the œsophagus of an Alsatian dog at Nairobi proved to contain *Spirocerca sanguinolenta* (Rud., 1819), the type species of the genus.

Fam.: *TETRAMERIDÆ* Travassos, 1914.
Sub-fam.: *TETRAMERINÆ* Railliet, 1915.

Genus: TETRAMERES Creplin, 1846.

The *Tetrameres* material consists of five females and two males of the cosmopolitan species *T. fissispina* (Diesing, 1861). They are from a chicken. The locality is given only as Kenya. The females were taken from the wall of the bird's proventriculus, while the males were free in its lumen. The swollen females are 2 mm. to 3 mm. in length by about 2 mm. diameter.

Fam.: *DIAPHANOCEPHALIDÆ* Travassos, 1919.

Genus: KALICEPHALUS Molin, 1861.

The *Kalicephalus* material was taken from the œsophagus, duodenum and small intestine of *Bitis* sp. (locality, Kabete) and from the intestine of *Naja nigricollis*, the spitting cobra, (locality, Ngong).

The specific diagnosis was very kindly made by Dr. R. K. Khanna, B.Sc., M.B. Two species are included.

Kalicephalus obliquus (Daubney, 1923). The specimens come from the œsophagus and small intestine of *Bitis*. Daubney's specimens were from *Bitis arietans*, *Bitis gabonica* and *Causus rhombestus*, all African snakes (1923, p. 71). Ortlepp (1923, p. 174) records *K. obliquus* from a colubrine snake (identity unknown) from Northern Nigeria.

Kalicephalus simus (Daubney, 1923). The worms are from *Naja nigricollis*. This is the type host from which the species was originally described by Daubney (p. 70). Ortlepp (p. 178) records it from the Black Mamba (*Dendraspis angusticollis*) in Nyasaland and the Congo.

With a view to indicating certain parasitic infections which may be expected among domesticated and other animals in East Africa, a list of the parasites described above, arranged under their respective hosts, is now appended.

CATTLE.—*Fasciola gigantica*. *Cotylophoron cotylophorum*. *Carmyerius exoporus*.

GOAT.—*Stilesia hepatica*. *Ostertagia ostertagi*. *Bunostomum trigonocephalum*. *Anoplocephalid* (immature).

SHEEP.—*Œsophagostomum columbianum*. *Hæmonchus contortus*.

HORSE.—*Strongylus equinus*. *Habronema muscæ*.

ZEBRA.—*Anoplocephala magna*. *Anoplocephala perfoliata*. *Triodontophorus tenuicollis*. *Crossocephalus viviparus*.

GAZELLE.—*Trichuris spiricollis* n. sp.

PIG.—*Cysticercus cellulosæ*.

DOG.—*Dipylidium caninum*. *Spirocerca sanguinolenta*.

JACKAL.—*Tænia* sp. (immature).

FOWL.—*Raillietina* (*Raillietina*) *tetragona*. *Raillietina* (*Paroniella*) sp. *Ascaridia styphlocerca*. *Ascaridia galli*. *Tetrameres fissispina*.

"COOT" (*?=Podiceps* sp.).—*Tatria decacantha*. *Tatria fuhrmanni*, n. sp. *Hymenolepis multistriata*.

RAIN EAGLE.—*Porrocæcum angusticolle*. *Ascaridia* sp. *Habronema* sp. inq.

PIGEON.—*Ascaridia columbæ*.

SNAKES.—*Cysticercus* sp. (in *Naja nigricollis*). *Ophiotænia gabonica* (in *Bitis* sp.).

Polydelphis attenuata (in *Bitis*). *Kalicephalus simus* (in *Naja nigricollis*). *Kalicephalus obliquus* (in *Bitis*).

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Journal of Helminthology, Vol. x, No. 4, September, 1932, pp. 231-234.

On the Pathogenicity of the Stomach and Lung Worms of the Cat.

By T. W. M. Cameron, M.A., D.Sc., M.R.C.V.S.

(Lecturer in Helminthology in the University of Edinburgh and the Royal (Dick) Veterinary College.)

In 1890, Müller described, from the lung of the cat, a species of nematode which is now known as *Aelurostrongylus abstrusus*. In 1928, I was able to show that its true habitat was not the lung substance, but the pulmonary artery and its branches, and that its pathogenic action, was mainly, if not entirely, due to the presence of the developing eggs and larvæ distributed throughout the lung tissue by the blood stream.

In 1865, Leuckart described from the stomach of the cat another species of nematode which he called *Ollulanus tricuspis*. His cats however, were simultaneously infected with the lungworm, and he believed that the larvæ which he found in the stomach and intestine were the young stages of the stomach worm. Cobbold, in 1875, published a paper dealing with this species, stating that he had first seen it in Edinburgh, 35 years previously. His cats likewise had a dual infection, and he, following Leuckart, believed that the larvæ which he saw were those of Ollulanus. In a series of papers in 1926-27, I published an account of the morphology and life histories of these two parasites, showing that the life cycle of Ollulanus was direct, while that of Aelurostrongylus involved a mouse.

The females of *Ollulanus tricuspis*, which measure about one millimeter in length, are viviparous, the larva developing to the third stage in the uterus. When it leaves the uterus, it is vomited by the cat and infection of another cat occurs by the latter swallowing the infective larva contained in this vomit. These larvæ are never found in the intestine or the lungs, only in the stomach. The adults burrow into the mucosa of the stomach (Figs. 1 and 2) and beyond causing a local erosion of the mucosa and increased secretion of mucus, give rise to no further damage. The irritation of their presence is probably an operative factor in causing the

cat to vomit, although it must be remembered that vomition is a normal phenomenon in this animal.

The life cycle of the lung worm is quite different. The eggs laid in the blood vessels are carried to the lungs where they develop into larvæ. These escape from the nodules which they induce, and, passing up the bronchi, reach the exterior in the fæces. There, the larvæ are ingested by mice and in the latter animal, reach the infective stage in the connective tissue between the muscles and beneath the skin. Infection of the definitive host is brought about by swallowing the larvæ in the mouse. Presumably, the larvæ emerge from their cysts in the intestine of the cat, and penetrating the intestinal wall, reach the lymphatics. They pass to the thoracic duct and, via the heart, reach the pulmonary artery.

Only one account of the pathogenic action of this parasite has been published. Stirling (1877) believing that they were the larvæ of Ollulanus described their encystment in the lungs and their gradual degeneration. His " degenerated " larvæ were, of course, eggs in process of development, and his " encysted " larvæ, forms ready to leave the lungs in the manner already noticed. Stirling stated that macroscopically, the lung was studded with small roundish bodies about the size of a pin's head and visible to the naked eye, resembling the nodules in miliary tuberculosis. The pleura was thickened. Microscopically, the nodules were round in shape ; in the centre lay a worm which was encapsuled and surrounded by connective tissue cells. Owing to the then prevailing misconception of the life cycle of this worm, his interpretation of the pathological picture, was, of course, erroneous.

The egg, about 80μ long by 70μ broad, is oval in outline and possesses a thin shell similar to that of the hookworm. The ova are carried by the pulmonary artery to the small arterioles in the lung and sooner or later are arrested by the narrowing lumen of the vessel in which they find themselves. This method of distribution explains the regular occurrence of the developing eggs in all parts of the lungs (Figs. 3 and 4).

When the ovum, acting as a foreign body, is arrested, blood clot is formed around it and in consequence a portion of the lung more or less conical in shape is deprived of its direct blood supply. The pulmonary alveoli in this area quickly become filled with catarrhal cells and some of the alveoli may collapse. If the number of adult worms is considerable,

sufficient eggs may be produced at any one time to cause the immediate death of the cat, owing to a considerable amount of lung tissue becoming infarcted. If the process is not so extreme, the exudate is very quickly eliminated by way of the bronchioles and upper air passages (Fig. 5).

Organisation of the thrombus commences almost at once (Fig. 5) and proceeds so quickly that by the time the egg is ready to hatch only traces of the pathological changes remain (Fig. 7). As usual, organisation of the thrombus is brought about by proliferation of the endothelial cells giving rise to fibroblasts, degenerative changes having occurred in the cells enclosed in the thrombus (Fig. 5). Eosinophiles are absent and at the end of the process, fibrous changes are very slight.

If the egg reaches a smaller vessel of about its own diameter before it is naturally arrested, no blood clot is seen in sections cut in a plane transverse to the long axis of the vessel and, moreover, the nodule is correspondingly smaller. The nodule has essentially the same structure as already described (Fig. 6). The catarrhal cells, towards the centre of the mass are somewhat larger than those towards the periphery but the whole nodule may be well explained as the result of the blockage of the arteriole ; toxic changes, if present at all, are very slight.

The picture presented in the case of the lung worm is quite different from that caused by the Ascarid larvæ. In the latter case eosinophiles are frequent ; the damage and the permanent resulting effects are extensive. It is generally assumed that the passage of the Ascarid larva through the liver and lungs is a phylogenetic reminiscence of the time when an intermediate host was necessary. The pathological picture is quite in accord with this view. As a rule, it is not in the interests of a parasite to kill quickly or incapacitate its definitive host ; by so doing it would imperil its own existence and the continuation of its species.

On the other hand, the damage done to an intermediate host is often considerable, especially if the latter has to be eaten by the definitive host for the completion of the life-cycle. When through the process of evolution, the definitive host becomes also the intermediate host, this capacity for damage is not lost. Accordingly it is quite logical to believe that, while the damage done by adult Ascarids is largely accidental, that done by their migrating larvæ is a survival of the time when a separate vector was essential.

In the case of the lung worm of the cat, the stages found in this animal are those associated with the adult parasite and with the normal disposal of the eggs and larvæ. By analogy with other helminths, the hatching and passage to the exterior of the larvæ should cause the cat as little damage as possible. This actually is the case. The eggs induce a small thrombus and a consequent local catarrhal reaction in the neighbouring alveoli. Both of these lesions are quickly healed and little or no permanent damage results to the lung. The fact that the cat is killed when many adult worms occur simultaneously must be regarded as largely accidental from the parasite's point of view. The fact that neither a general nor a local eosinophilia occurs points to the fact that products toxic to the tissue are not elaborated by the parasite during this stage of its development and consequently supports this contention. Lastly, the fact that hæmorrhage in the neighbourhood of the occluded vessel is practically always absent must be due to the small calibre of the pulmonary arteriole affected.

I am greatly indebted to my colleague, Dr. F. E. Reynolds for his invaluable advice, assistance and criticism during the process of this investigation, and to Mr. W. A. McDonald for the microphotographs.

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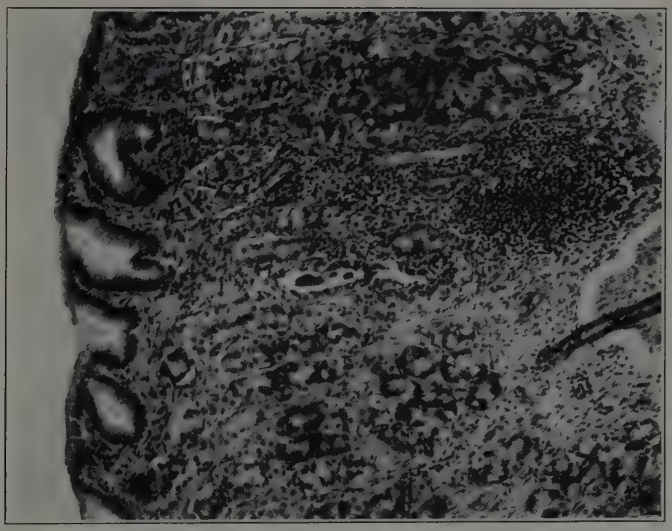

Fig. 1. Low-power photograph of a portion of the stomach of cat. An adult worm is seen in the centre of the field, just above the lymph nodule. (These large lymph nodules are normal features in the stomach of the cat.)

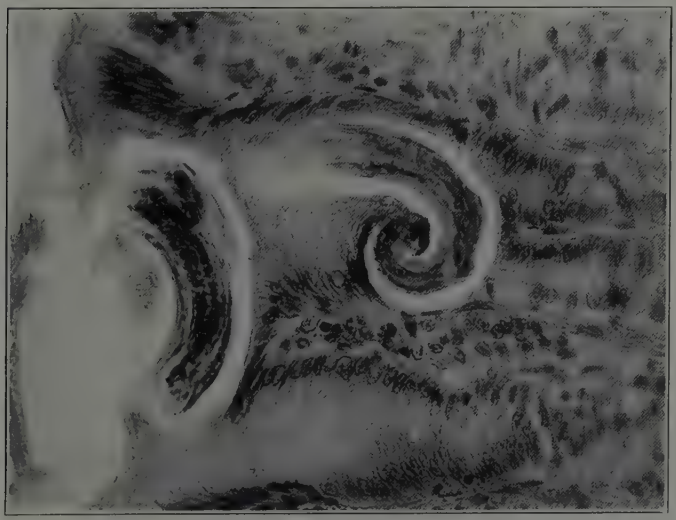

Fig. 2. High-power view of stomach of cat, showing the adult worm *in situ*. Two portions of the same worm appear in this section. There is an erosion of the mucosa where the worm has burrowed into it; the mucus glands are unusually active and an abnormal secretion of a thick, glairy mucus has occurred.

Ollulanus tricuspis (Figs. 1-2).

Facing page 234

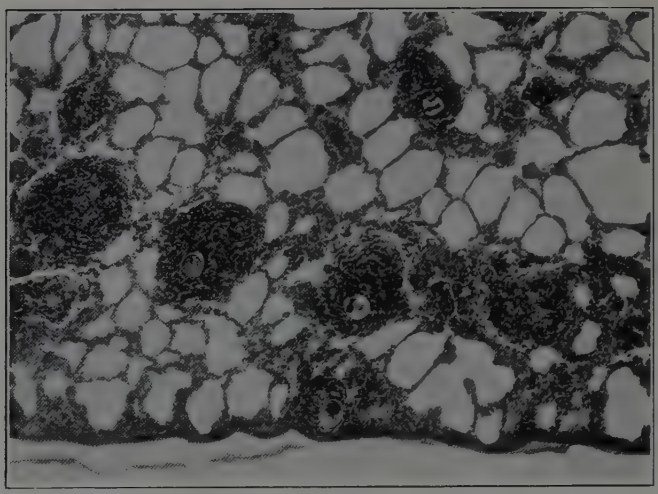

Fig. 3. Low-power view of a peripheral portion of the lung of the cat, showing the general distribution of the lesions.

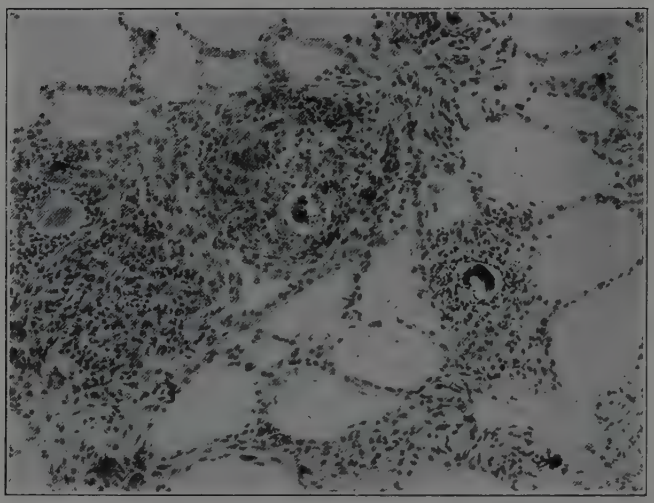

Fig. 4. A moderately high magnification of the same lung showing eggs in various stages of development.

Aelurostrongylus abstrusus (Figs. 3-8).

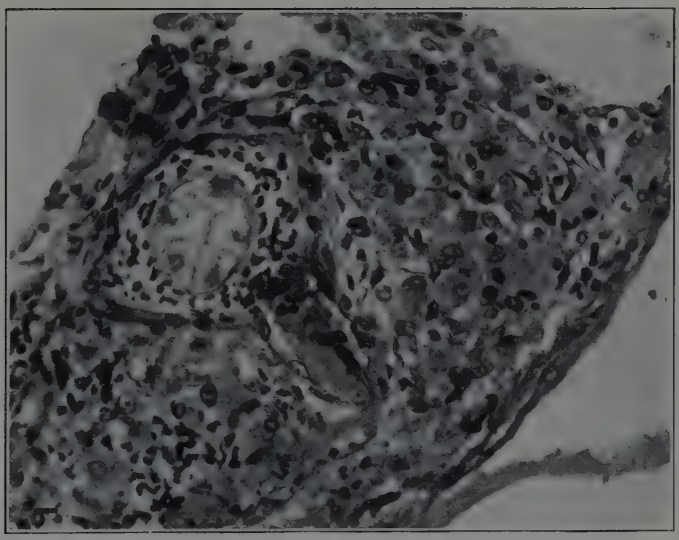

Fig. 5. Egg in an early stage of development, enclosed in a thrombus in an arteriole slightly larger than itself. The egg is surrounded by disintigrating leucocytes, while towards the pleural surface of the lung, a thrombus undergoing early resolution may be seen. The surrounding alveoli are filled with a catarrhal exudate.

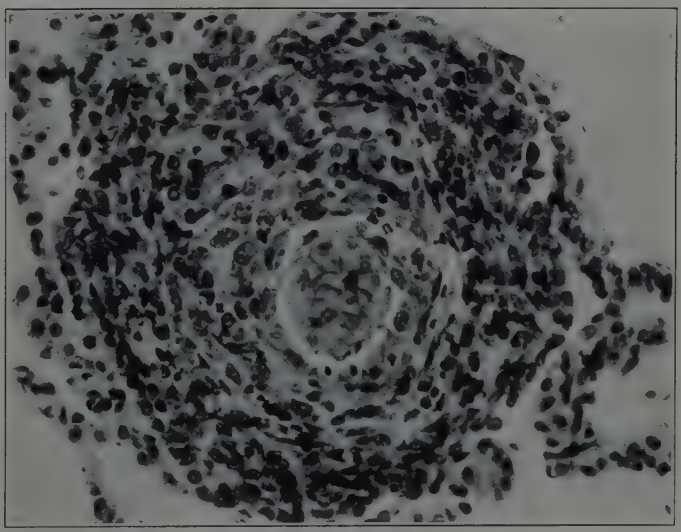

Fig. 6. Egg in a similar stage of development in a small blood vessel which it almost entirely occludes. It is surrounded by a catarrhal exudate and collapsed alveoli.

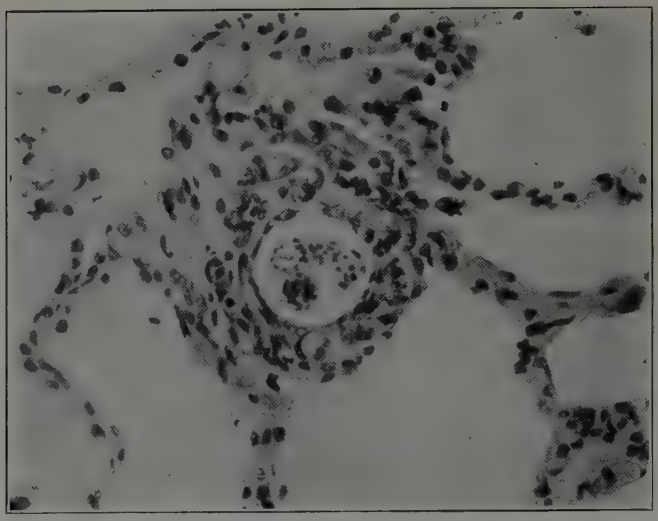

Fig. 7. The egg contains a larva and is considerably older than the stages seen in figures 5 and 6. The catarrhal exudate produced by the initial trauma has almost entirely disappeared.

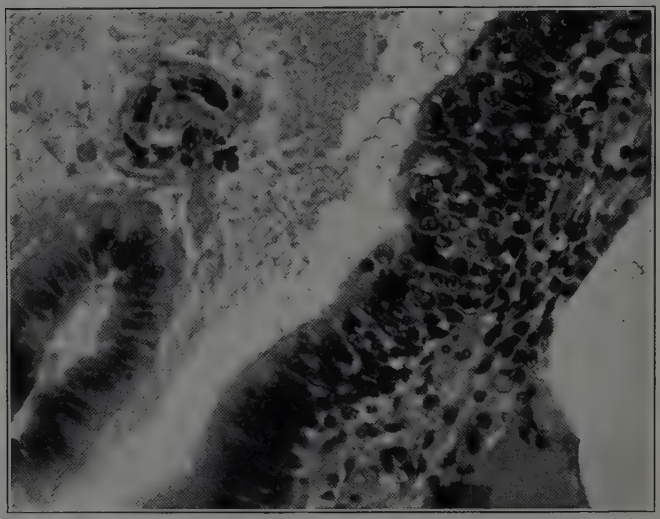

Fig. 8. Small bronchus of a cat containing exudate from the pulmonary alveoli A larva is seen on the wall of the bronchus on its way to the exterior.

Index to Vol. X.

Index of Authors.

NEW SPECIES IN VOLUME X.